

I Thallophyta - Thallus plant.
Algae

II Bryophyta - moss plants
Lungi

III Pteridophyta - Fern plants.

IV Spermatophyta
Class 1 - Gymnospermae - Conifers
Class 2 - Angiospermae
Subclass - Dicotyledons
" " - Monocotyledons

Order
Families
Genera
Species.

ELEMENTS OF BOTANY

BOTANY TEXTS

ELEMENTS OF BOTANY

By RICHARD M. HOLMAN, Associate Professor of Botany in the College of Letters and Science of the University of California; and WILFRED W. ROBBINS, Professor of Botany in the College of Agriculture of the University of California. 380 pages. 5½ by 8½. 241 figures. Cloth.

TEXTBOOK OF GENERAL BOTANY

For Colleges and Universities. By RICHARD M. HOLMAN and WILFRED W. ROBBINS. Second Edition, 624 pages. 6 by 9. 415 figures. Cloth.

LABORATORY GUIDE FOR A COURSE IN GENERAL BOTANY

By LEE BONAR, RICHARD M. HOLMAN, and LUCILE ROUSH, all of the Department of Botany of the University of California. 106 pages. 6 by 9. Cloth.

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BY

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Science of the University of California*

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PREFACE

IN August, 1924, the authors published "A Textbook of General Botany for Colleges and Universities," which was designed for a year's course. The Second Edition of this text came from the press in October, 1927. Since the issuance of this book, there has arisen a need for a text which would embody the same material, the same organization and viewpoint as that of the "Textbook of General Botany," but so abridged as to fit it especially for use in institutions in which only one semester is devoted to the course in general botany, or in which, for other reasons, the subject is less extensively studied than in those colleges and universities for which the larger book is particularly fitted. The authors have attempted to meet this need by the preparation of the present book.

A number of illustrations have been borrowed from various sources and are acknowledged in the legends.

Credit is due Miss Helen Mar Wheeler for proof-reading.

RICHARD M. HOLMAN.

WILFRED W. ROBBINS.

BERKELEY, CALIFORNIA,

May 11, 1928.



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CONTENTS

	PAGE
PREFACE	v
CHAPTER	
I. THE PLANT BODY	1
II. THE CELL	17
III. THE STEM	42
IV. THE ROOT	80
V. THE LEAF	99
VI. THE FLOWER	133
VII. FRUIT AND SEED	155
VIII. RELATION OF THE PLANT TO ENVIRONMENT	180
IX. THE PRINCIPAL PLANT GROUPS	197
X. THALLOPHYTA—ALGAE	203
XI. THALLOPHYTA—FUNGI	229
XII. BRYOPHYTA (LIVERWORTS AND MOSSES)	270
XIII. PTERIDOPHYTA (FERNS AND FERN ALLIES)	288
XIV. SPERMATOPHYTA (SEED-BEARING PLANTS)	307
XV. EVOLUTION AND HEREDITY	343
INDEX	361

ELEMENTS OF BOTANY

CHAPTER I

THE PLANT BODY

THE activities of the individual plant are two-fold: **vegetative** and **reproductive**. Vegetative activities are those which have to do with the growth and preservation of the individual. The principal vegetative activities or functions of the plant are absorption of raw materials from the soil and atmosphere, transfer of the raw materials and of food in the plant body, manufacture of food, assimilation (the process by which foods are transformed into the living material—protoplasm), respiration (a “breaking down” of substances in the cell, which provides energy for the work of the plant and in which oxygen is taken in and carbon dioxide given off), and transpiration (water loss). Reproductive activities are those which have to do with the preservation of the species to which the individual belongs.

Organs and Tissues.—We speak of the human body as being made up of a number of organs, each with a work to do. There are organs of sight, of hearing, of digestion, etc. Just so, we may speak of the **plant body**. It, too, is composed of various organs, with which it carries on its different activities. An organ is a part or member of the plant with a particular kind of work to do. For example, the roots are absorbing and anchoring organs, the stems conducting and supporting organs, the leaves food-making and transpiring organs, and the flowers are reproductive organs. If we study microscopically the structure of organs, we find they are composed of many small bags or sacs the walls of which are

usually thin and transparent. Each of these microscopic sacs or compartments is called a cell. Just as a brick wall is made up of separate units, the bricks, so is the plant body made of separate units, the cells. It is in the cells that all the complex physical and chemical changes of the living body take place. Cells of similar structure which together perform a special function constitute a tissue. Thus an organ such as the leaf is composed of several different kinds of tissues, including in this case, conductive tissues, protective tissues, and food-making tissues.

Some plants have but few distinct organs, or a only few tissues, with which to carry on the different functions. Such plants are said to be simply organized. Examples are the pond scums, seaweeds, molds, mildews, rusts, smuts, etc.

Many plants have numerous distinct organs and many tissues to carry on the separate functions. This is true of the more familiar plants of orchard, garden, field and forest. Such plants are said to be highly organized.

Since an organ is an adaptation for a particular function there is the closest interdependence between its structure and its function. Neither can be fully understood without reference to the other. Similarly one must hold in view the interrelations between the several organs and their functions with reference to the plant body as a whole.

The truth of the last statement is reflected in the subdivisions of botany. While they are mainly conveniences for the purposes of research or of advanced study, each centering attention on some part or aspect of the plant, they are all more or less closely interdependent. Structure is treated by plant morphology: the grosser form and organization by external morphology, the more minute internal structure (mainly microscopic) by histology. Histology includes anatomy, which deals with the framework formed by the cell walls, and cytology, which deals with the cell protoplasm, the living material sustaining all life processes or activities of the plant. These life processes are studied by plant physiology, a special branch of which, plant ecology, deals with

the relations of plants to their environment. Systematic or taxonomic botany classifies and describes plants. The foregoing comprise pure botany, whose scientific results are put to practical use by applied botany, as in horticulture, agronomy, etc.

Kinds of Plant Bodies.—The plant body may consist of a single cell which carries on all the life activities. Among such simple unicellular plants are the bacteria (Figs. 149 and 150) and *Protococcus* (Fig. 132). Great numbers of the latter constitute the green growth commonly found (in the northern hemisphere) on the north side of tree trunks, fence posts and walls. A plant body in which cells are joined end to end to form a thread or filament represents an advance in complexity over the unicellular forms. There are many thread-like algae, such as *Spirogyra* (Fig. 134), one of the pond scums, and *Oedogonium* (Fig. 139); and also many filamentous fungi. In *Oedogonium* there is a slight degree of specialization, in that some cells may become differentiated for special functions. In some of the seaweeds (*Ulva*, or sea lettuce, for example), the plant body is a flat plate two cells thick. In other more complex seaweeds (Figs. 143 and 144) and in such fungi as mushrooms (Fig. 176) there is a rather complex and extensive plant body, but in none of the fungi or algae are there true stems or leaves.

The Plant Body of Seed Plants.—In the plant body of seed plants (Fig. 1) the stems, foliage leaves, and roots are chiefly concerned with carrying on the vegetative functions, whereas the flowers, which produce seeds, carry on the reproductive activities.

The plant body of the seed plant is made up of shoot and root.

The shoot, which is made up of two kinds of organs, stems and leaves, generally grows upwards into the air, whereas the root grows downward into the soil. The stem is divided into nodes and internodes. Nodes are slightly enlarged portions where leaves and buds arise and branches originate. An internode is the region between two successive nodes.

Principal Distinctions between Stem and Root.—Stems and roots are both cylindrical structures which, in some cases, are

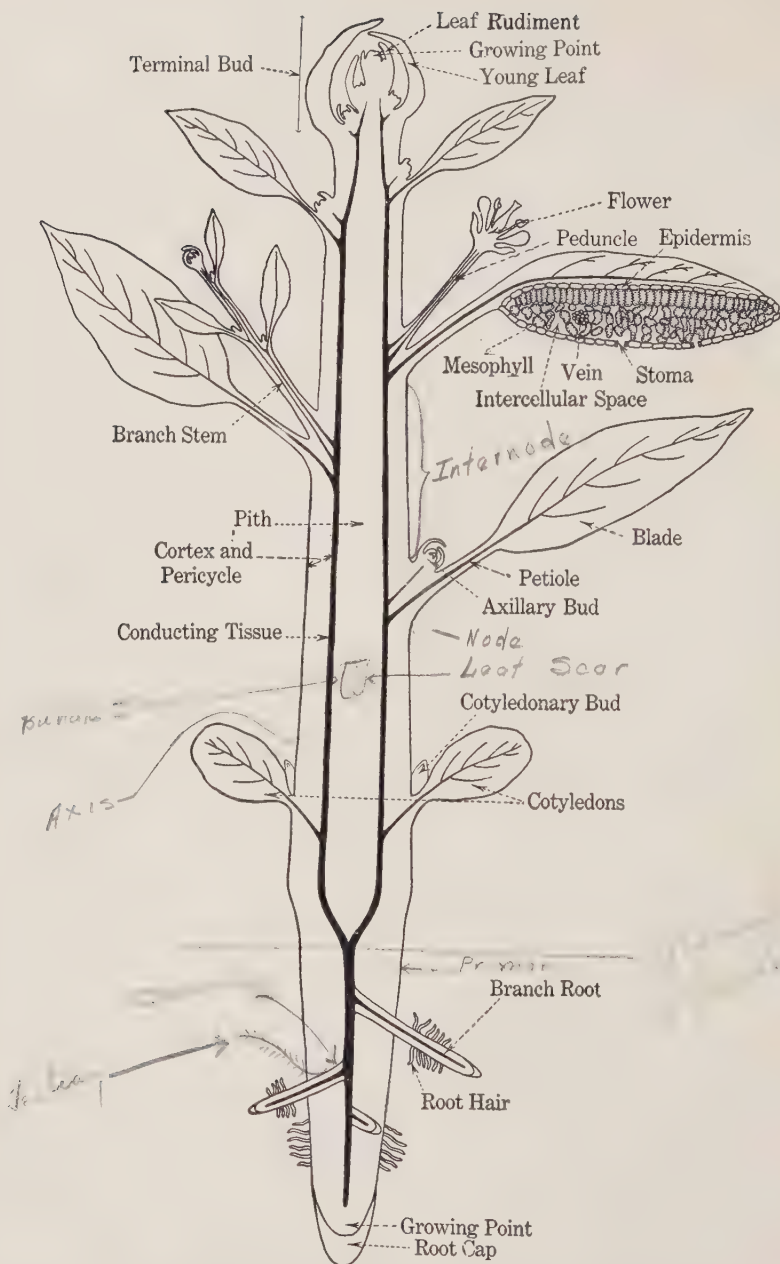


FIG. 1.—Diagram of a seed plant showing the principal organs and some of the tissues. (Modified after Sachs.)

difficult to distinguish from each other. Their principal differences are:

(1) Normally, branch stems arise only in the **axils** of leaves at nodes (the axil is the upper of the two angles which the leaf stalk forms with the stem to which it is attached). Roots, on the contrary, branch irregularly, not being divided into nodes and internodes.

(2) The internal structure of the stem differs from that of the root.

(3) Stem branches originate at the surface of a main stem and near its extreme tip; branch roots arise, not at the surface, but within a larger root and at some distance from its tip.

(4) The **growing point** of the stem is covered and protected by rudimentary foliage leaves and in some cases by modified leaves, the **bud scales**. The growing point of the root, however, is protected by a special thimble-shaped structure, the **root cap**.

Functions of Stem, Root, and Leaf.—The primary functions of the stem are (1) the **support** of foliage leaves and flowers; (2) the **conduction of raw materials** (water and mineral salts from the soil); and (3) the **conduction of plant foods** from the points where they are manufactured to points where they are needed in growth or where they will be stored for future use.

In addition to these primary functions, stems perform diverse secondary ones. Green stems supplement the leaves in food manufacture. In some plants stems act as storage organs, of starch, for example, in the potato, and of water in cacti, or they may act as organs of vegetative reproduction, as do the tubers (enlarged underground stems) of the potato, the bulbs (short stems with fleshy leaves) of the onion, the runners (creeping stems) of the strawberry, the rhizomes (underground stems) of the Canada thistle, etc.

The primary functions of the root are (1) **anchorage**, and (2) **absorption of raw materials** (water and certain mineral salts from the soil). A secondary function is food storage. Common

examples of roots which act as storage organs are those of sugar beet (*Beta vulgaris*), turnip (*Brassica rapa*), and sweet potato (*Ipomoea batatas*).

The primary functions of the leaf are the **manufacture of carbohydrates** (photosynthesis) and **transpiration** (loss of water in the form of water vapor).

General External Features of the Shoot, Especially of Woody Plants.—Three general types of shoots are recognized: **Erect**, **prostrate**, and **climbing**. The shoots of most plants grow erect, but the shoots of such plants as the cucumber, squash, watermelon and strawberry are prostrate on the ground. Plants which climb upon other plants and depend upon them for mechanical support, that is plants with climbing shoots, are known as **lianas**. Examples of lianas are the scarlet runner bean (*Phaseolus*), dodder (*Cuscuta*), hop (*Humulus*), and grape (*Vitis*).

There are two principal forms of erect shoots, **excurrent** and **deliquescent**. Pines, spruces and firs have a single main stem with many lateral branches. So also in the Carolina poplar there is a "leader"—one main stem which remains the principal stem throughout the life of the plant. This type of shoot is said to be **excurrent**. In the oak, common cottonwood, apple, and many other kinds of trees, the principal stem does not continue through to the top of the tree but is replaced above by several large branches so that it is impossible to pick out any one main stem. Such shoots are spoken of as **deliquescent**.

Buds.—A bud consists of a short length of partially developed stem with rudimentary leaves in various stages of development. That it is actually a shoot becomes clear when we cut the bud lengthwise and study its structure. It is also shown by the fact that branches always develop from buds. In many species of plants buds may be removed from the stems on which they originated and with certain precautions set into the stems of other plants where they will subsequently develop into branches. Such **bud grafting** is a common horticultural practice.

The delicate growing point (extreme tip of the stem within

the bud) and the rudimentary leaves, especially in trees and shrubs of cold and arid climates, are usually protected by several layers of overlapping scales (**bud scales**) which are modified leaves (Fig. 2). Bud scales may be covered with hairs, as in the willow, or with a waxy secretion, as in the cottonwood. These coverings very effectively protect the enclosed tender parts from rapid drying out as well as from mechanical injury. Naked buds are not protected by scales; they are found on woody plants of the moist tropics, and on herbaceous plants the world over.

Buds may be classified (1) as to their position on the stem, (2) as to the number at a node, (3) as to the structures which they contain, and (4) as to their development.

(1) Buds may be classified as to their position on the stem into: (a) terminal, (b) axillary, and (c) adventitious.

(a) Most branches end in a bud which is called the **terminal bud** (Figs. 1, 3, and 22). As a rule, the stem which develops in a single season from a terminal bud is longer than any of those which develop from other buds on the same branch.

(b) **Axillary buds** are buds which arise in leaf axils, that is, just above the place on the stem where a leaf is attached. They may give rise to leafy branches or to flowers. On very short branches (spurs) it is sometimes difficult to distinguish between

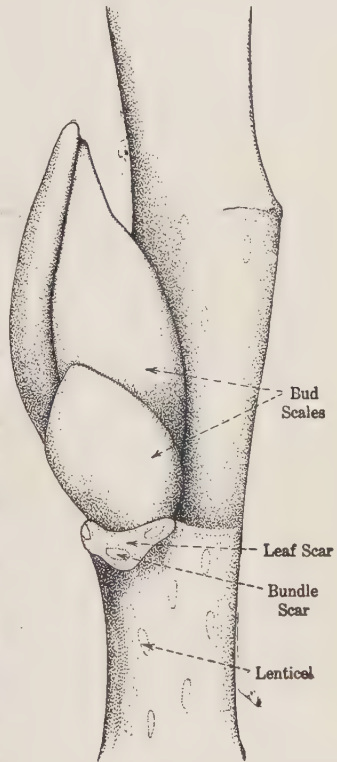


FIG. 2.—External view of a portion of a cottonwood stem showing an axillary leaf bud, leaf scar and lenticels.

terminal and axillary buds. Accessory buds, which are well illustrated in the maples and box elder (*Acer*), are extra buds developed in the leaf axils in addition to the single axillary bud proper.

(c) **Adventitious buds** are buds which arise anywhere on the plant except at the tip of the stem or in the leaf axils. They may arise on stems or roots, or even leaves. Their formation is usually stimulated by injury. For example, when a branch is cut back, as in pruning, numerous adventitious buds may arise at the edges of the cut surface.

(2) Axillary buds may be classified **as to the number at a node** into: (a) alternate, (b) opposite, and (c) whorled. When one bud occurs at each node, as in the apple, peach, plum, and cottonwood, they are said to be alternate. When there are two buds at a node, on opposite sides of the stem, as in the mints, box elder, and maples, they are opposite. When more than two buds occur at each node, as in catalpa, they are said to be whorled.

(3) **As to the structures which they contain**, buds may be (a) leaf, (b) flower or fruit, or (c) mixed buds. When a **leaf bud** is opened there is found a much shortened axis or stem bearing a number of small leaves; since by elongation it may develop into a leafy branch, an axillary leaf bud may as properly be called a **branch bud**. The new branch stem, just as the old one from which it came, has buds in the axils of its leaves and itself ends in a terminal bud.

A **flower or fruit bud** is one containing flower parts but no foliage leaves. If we open a bud of this type, we find one or more young, unexpanded flowers. Fruit buds are rarely terminal, as in the loquat (*Eriobotrya japonica*), but are commonly axillary as in the peach and cherry (*Prunus*), in gooseberry (*Ribes*), and walnut (*Juglans*).

A **mixed bud** is one that contains both flowers and leaves. When a bud of this type unfolds there is produced a leafy shoot which either (a) terminates in a flower cluster, or (b) bears flowers or flower clusters in the leaf axils. The first mentioned

type of mixed bud is characteristic of the apple, pear, blackberry (*Rubus*) and grape (*Vitis*), and many others; whereas the second type is found in the persimmon (*Diospyros*), mulberry (*Morus*), fig (*Ficus*), oak (*Quercus*), and a number of others.

(4) Buds may be classified, **as to their development**, into (a) **active** and (b) **dormant** buds. An active bud is one which develops into a new branch stem or (in the case of terminal buds) into an elongation of an already existing stem. Dormant buds are those which remain undeveloped for one or more seasons after they are formed.

As noted before, the terminal bud of a branch is almost always the most active and grows more vigorously than any of the axillary buds. The axillary buds frequently decrease in activity with their distance from the terminal bud. Buds several internodes distant from the apex of the stem are generally dormant and normally do not develop at all into branches. In most plants the removal of a terminal bud or of the upper end of a branch stem increases the activity of the remaining axillary buds, and as a result some of the dormant buds may become active. Such "awakening" of dormant buds is the less complete the further the buds are down the stem. Thus it may be said that generally the degree of activity of active buds decreases and the "depth" of dormancy of dormant buds increases the greater the distance from the end of the branch.

Many buds which are apparently adventitious are often in reality axillary buds which have remained dormant so long that their original position relative to a leaf, long since shed, is difficult to ascertain.

The branching system of the shoot is determined largely by the arrangement of the buds; thus plants with alternate buds have branches also alternate but much less constant and regular in their alternate arrangement than are the buds, for many buds remain dormant, and of the active buds some die of the attacks of insects or disease, while others fail in the competition for light and food and do not develop further.

It is a common and well-known practice of orchardists and

gardeners to change the form of plants while they are still young by pruning, which is the judicious removal of buds or branches. The removal of terminal buds or terminal portions of branches will stimulate the development of axillary buds, cause a spreading of the plant, and thus produce a broad tree with a "low head." A cylindrical or pyramidal type of tree may be secured by removal of a certain number of lateral buds or branches.

The Stems of Woody Deciduous Plants in their Winter Condition.—A several-year-old twig of such a plant (cottonwood) is illustrated in Fig. 3. At the tip is the large terminal bud and at each node there is an axillary bud. If the brown scales are removed from either type of bud young overlapping foliage leaves will be exposed. Within some of the axillary buds partially developed flowers may also be found. Below each bud is a semicircular or elliptical

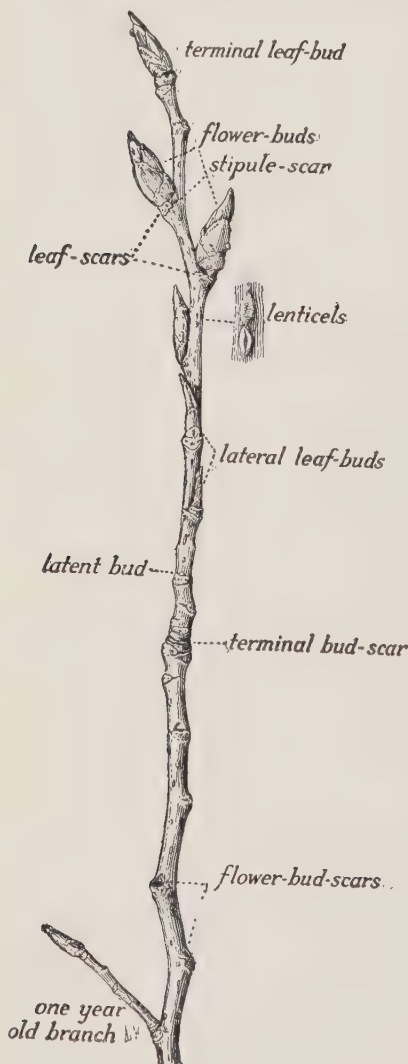


FIG. 3.—Two-year old cottonwood twig after the leaves have been shed. (From Robbins' *Botany of Crop Plants*, after Longyear.)

leaf scar. This was left when the leaf, in the axil of which the bud was formed, became detached from the twig. The number of these scars at a node shows whether the leaves were alternate, opposite or whorled in arrangement.

The twig's growth in length during each year is marked by the successive rings of **bud scale scars** left when the close-set bud scales of the terminal bud are shed in the spring. The spacing of these rings often reveals striking differences in the amount of growth produced each year, for there is practically no increase or decrease in the length of any portion of a stem after that portion is a year old.

On some twigs flower bud scars may also be found where the short branch which developed from a flower bud became detached from the stem after the fruit had matured.

Close examination of the surface of the twigs where there are none of these various kinds of scars will reveal numerous lighter colored, slightly raised spots on the bark. These are **lenticels**, regions which permit the passage of gases inward and outward. Except for these lenticels the bark would almost completely prevent the passage of air or water (as a liquid or as vapor) into or out of the stem.

Modified Stems and Roots.—Roots, stems, leaves and flowers are not always typical, but may be modified in some cases to such an extent as to be scarcely recognizable. For example, the tendril of the sweet pea (*Pisum sativum*) is morphologically a leaf part; the Irish potato tuber, a modified stem; the sweet potato, a modified root.

Some seed plants do not possess all of the usual parts of the plant body, namely, roots, stems, leaves and flowers. For example, in the common water bladderwort (*Utricularia vulgaris*) the roots are wanting; in the floating *Wolffia*, both leaves and roots are absent; and in *Rafflesia arnoldii*, a tropical parasite which has the largest flowers of any plant in the world, the plant is reduced to a flower and a mass of undifferentiated cells within the tissue of the host.

Stems may be in the air (**aerial**) or underground (**subterranean**). The stems of most seed plants are aerial. However, in such plants as common Irish potato and Canada thistle there are stems underground as well as above ground.

Factors Which Determine the Direction of Growth of Different Parts of the Plant Body.—*Geotropism*.—In most plants the

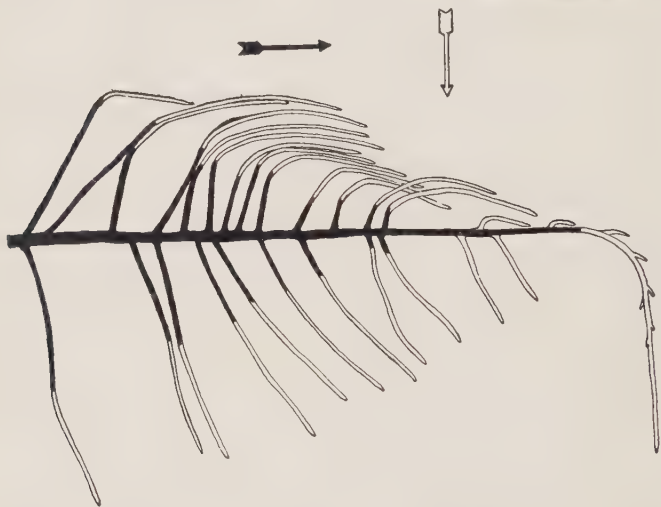


FIG. 4.—Diagram of the root system of the broad bean (*Vicia faba*) showing the geotropic curvature of the secondary roots and of the primary root. Originally the whole primary root was growing parallel to the direction of gravity, shown by the solid black arrow. Then the root system was turned through 90° so that it was at right angles to the direction of gravity (outlined arrow). Growth of the root system before and after the change of position are indicated respectively by solid black and outline portions of the figure. The secondary roots do not tend to grow straight downward like the primary root but obliquely downward.

main stem tends to grow vertically upward, and when there is a single primary or tap root that root tends to grow vertically downward. On level ground the direction of growth is thus generally at right angles to the surface. On a slope, however, it is clear that the stem is not at right angles to the surface of the soil but that it tends to be truly perpendicular, that is, following a radius

of the earth. Regardless of the slope of the land the tap root also tends to grow perpendicularly, but in the opposite direction from the main stem.

When a seedling, or an older plant having a single primary root and one main stem, is placed in a horizontal position the

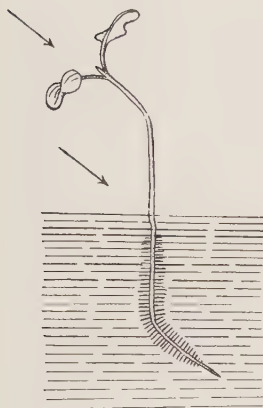


FIG. 5.

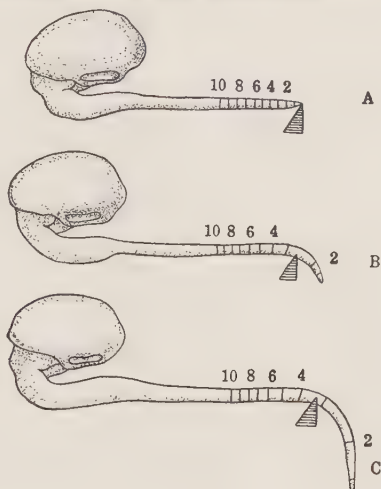


FIG. 6.

FIG. 5.—Mustard seedling growing in water showing the positively phototropic curvature of the hypocotyl and the negatively phototropic curvature of the root. The arrows show the direction from which light is falling upon the plant. (After Sachs.)

FIG. 6.—A seedling of white lupine (*Lupinus albus*) (A) at the time it was placed in the horizontal position, and (B and C) after a shorter and longer period in the new position. The end of the root is marked off into zones beginning with the extreme tip of the root and each originally one millimeter long. Note that the region of curvature corresponds with the region of most rapid elongation and that the sensitive region (included in the first two millimeters) is not elongating much at the time of the curvature. (Redrawn from Sachs.)

growing region of the root will bend until it points downward and the growing portion of the stem will curve upward. This orientation of stem and root is a response to gravity and is called **geotropism**. It is a very remarkable fact that the same stimulus

(gravity) is responded to by the roots and by the stem with exactly opposite **reactions**. Organs which, like the root, bend downward when displaced from their normal position are said to be **positively geotropic**, while those which bend upward are spoken of as **negatively geotropic**.

Phototropism.—If a house plant is placed at some distance from a window the growing part of the stem will tend to curve toward it. Actually it will not grow directly toward the light because geotropism will tend to keep it growing perpendicularly upward. The direction in which it grows will be the resultant of two tendencies: (1) the tendency to grow parallel to the direction of gravity, and (2) the tendency to grow parallel to the direction of the illumination. The adjustment of various plant parts relative to the direction from which light falls upon them is called **phototropism** (less accurately **heliotropism**). The main stems of most plants are **positively phototropic** (turning toward the strongest illumination), while the primary roots of a few plants have been shown to be **negatively phototropic** (turning away from the strongest illumination). Leaves also are commonly phototropic, but they generally so adjust themselves that the leaf surface is not parallel to, but approximately at right angles to the direction of the light which falls upon them.

Other Tropisms.—Gravity and light are the most important of the external factors which determine in what direction plant parts shall grow. Other such factors of less importance are (1) differences in the quantity of moisture in the medium surrounding the organ in question, (2) differences in the concentration of certain other substances in the medium, (3) differences in temperature in the medium, (4) contact with some solid object, and (5) movement of water in which certain plant organs may be growing.

The Life Cycle.—Every plant, like every animal, begins its life as a single cell. In the simplest plants, like bacteria and certain blue-green algae, this single cell is the individual plant itself. It divides, resulting in two individual one-celled plants; these in

turn grow and divide, and so on. The **life cycle** of such a plant is short and simple. In the higher plants like wheat (*Triticum*), the beet (*Beta*), and the apple (*Pyrus*) the life cycle is much more complex and of longer duration. According to their length of life, plants may be classified as annuals, biennials and perennials.

An **annual** is a plant which completes its life cycle within one year's time. In wheat, for example, the seed germinates, roots, leaves and stems are produced, and in one season the plant reaches adult size. After this relatively brief period of vegetative activity, flowers and seeds are produced and within each seed there develops a rudimentary wheat plant, the embryo of the seed. The parent plant then dies. Thus the life cycle of this annual plant is completed. In cool climates certain plants behave as **winter annuals**. In these cases the seeds germinate in late summer or fall, the young plants live throughout the winter and the following spring send up flower stalks, blossom, and bear seed.

A **biennial** is a plant which completes its life within two years and then dies. The beet plant may be taken as a type of the biennial. The embryo plant resumes its growth at the germination of the seed, and during the first season produces a number of large leaves crowning a fleshy root, the "beet." In contrast with the annual, no flowers and seed are produced the first year; instead the plant is engaged chiefly in storing food in the root. In the fall the leaves die, but the "beet" (root) remains alive, except in regions of severe winters where they must be dug and stored to protect them from freezing. The next season the "beet" sends up a shoot three or four feet high, which gives rise to flowering branches. Seed is finally produced, and soon afterward the plant dies. As in the case of the wheat plant, the beet plant has but one period of seed production, after which the whole plant dies, but the beet, like all other biennials, requires two vegetative seasons to complete its cycle, whereas the wheat plant requires but one.

All the familiar trees and shrubs are good examples of plants which live more than two years. Thus in the apple, after seed

germination there is a succession of growth periods during which there is no production of flowers and seed. At the age of four or five years flowers and seed are produced, from which time forward the tree continues both vegetative and reproductive activities for many years. Such plants are said to be **perennial**.

CHAPTER II

THE CELL

IF we cut a thin slice from a root, stem, leaf or any other living plant structure and examine it under the microscope we find that it is made up of many small chambers separated from each other by walls which are generally thin and transparent. Within each of these compartments there is a small quantity of

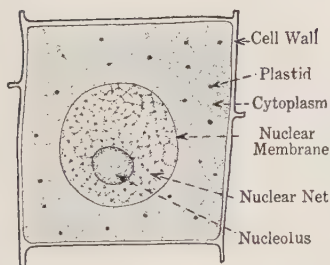


FIG. 7.—A cell from the meristematic tissue of the growing point of a root of onion (*Allium cepa*).

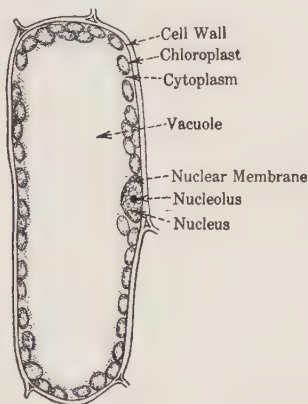


FIG. 8.—A cell from the palisade parenchyma of a leaf.

a viscous, almost transparent substance. This is **protoplasm**, the living material of both plants and animals. These masses of protoplasm with their surrounding walls are called **cells**. The protoplasm within a single cell cavity is called a **protoplast**. Cells are in fact the units of structure and function in all organisms. They vary greatly in size, but in relatively few cases is the longest diameter greater than 0.25 millimeter or less than 0.025

millimeter. Plant cells differ greatly in their shape, in the thickness of their walls, and to a certain extent in the nature of the material of which the walls are made. The structures which are found within the protoplasm are far from uniform in number, form, and size.

Most plants are multicellular, that is, are composed of many cells, hundreds, thousands or even millions of them, and their organs are generally also multicellular. Yet every function which the plant performs is but the expression of the activities of individual cells, and in unicellular (one-celled) plants all of the essential life processes may be carried on within a single protoplast.

The Cell Wall.—The wall is secreted by the protoplast. When the cells are young the wall is very thin, but as they grow older successive layers of new cell-wall material are added and the wall may finally come to have a thickness many times as great as when it was first formed. The original thin wall separating two adjacent protoplasts is called the **middle lamella**. It is composed largely of a substance called pectose or of calcium pectate, a compound of pectic acid and lime. The rest of the cell wall generally consists of almost pure cellulose, a compound belonging to the carbohydrates. Cane sugar, glucose or grape sugar, and starch are other familiar examples of carbohydrates. Pectose easily changes into pectin, a substance which causes fruit jellies to stiffen when present in sufficient quantities and accompanied by proper proportions of fruit acid and sugar. Cellulose is of great economic importance. It gives us cotton, linen, hemp, and wood; fodder for cattle and other herbivorous animals, and raw materials for the manufacture of gun cotton and other explosives, celluloid, and artificial silk.

The Protoplast.—The term protoplast is a useful designation for the mass of living material, or protoplasm, found within a single cell cavity.

Protoplasm is not a single chemical compound like the cellulose of the cell wall, but a mixture of many different com-

pounds. These include carbohydrates, water, fatty substances, proteins, and simple compounds of phosphorus and sulphur and of the metals, calcium, potassium, and magnesium. Proteins are present in larger quantities than any of the other substances excepting water. Familiar examples of proteins are gelatine and egg white. In addition to carbon, oxygen and hydrogen,

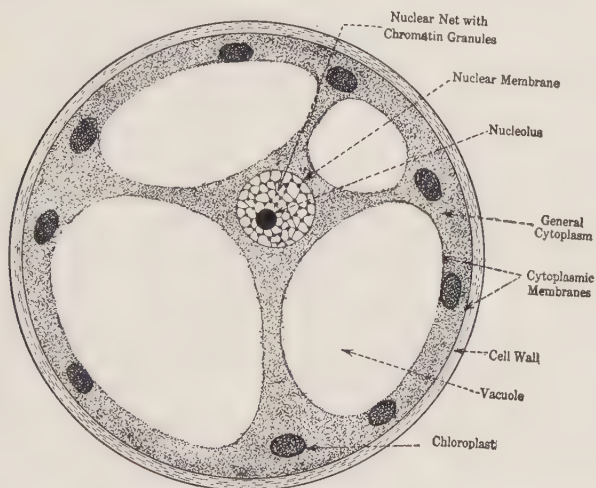
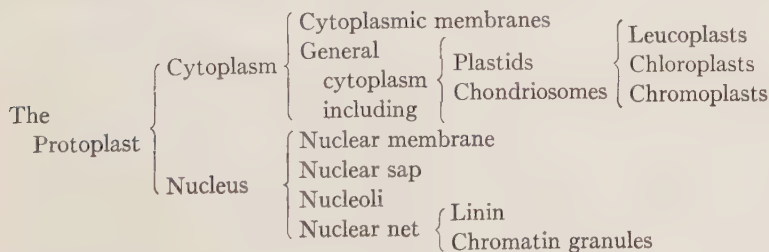


FIG. 9.—Diagram of a single-celled (unicellular) green plant, showing the cell wall, the vacuoles, and the relation of the different parts of the protoplast.

the proteins contain nitrogen and sulphur, and in some cases phosphorus also.

The different parts of the protoplast and their relation to each other are shown in the following outline:



The Cytoplasm.—Except in the case of the blue green algae and bacteria there is in the protoplast of every typical cell a round or oval structure called the **nucleus**. All of the protoplasm outside of the nucleus is called **cytoplasm**. In most cases the cytoplasm forms the greater part of the protoplast. Embedded in it are non-protoplasmic bodies of a number of different kinds. They are called **inclusions**. The most common of these are the **vacuoles**, which are nothing more than drops of a watery solution of various substances. Vacuoles vary greatly in size. They sometimes make up half or more of the volume of the cell. Where the cytoplasm is in contact with the cell wall there seems to be a thin layer having quite different properties from the rest of the cytoplasm. For this bounding membrane we shall use the term **cytoplasmic membrane**. Where the cytoplasm is in contact with a vacuole there is a similar cytoplasmic membrane. These membranes are thought to be of very great importance because they probably control the entrance and exit of substances into and from the cell. They are **semi-permeable membranes**, that is to say, membranes which will permit the free passage through them of water and of certain substances in solution, but which prevent, or at least very greatly hinder, the passage of certain other substances in solution.

Plastids.—In many cells there are specialized, living, cytoplasmic structures, called plastids. These are generally spherical or ellipsoidal in form and may be considered merely as portions of the cytoplasm which are specially differentiated to perform particular functions in the cell. The plastids are of three kinds, which differ in color and in the nature of the work which they perform. There are green plastids, which are called chloroplasts; colorless ones known as leucoplasts; and chromoplasts, which may be various degrees or combinations of yellow, brown or red. The term **chromatophore** is often used to include all colored plastids. The color of the chloroplasts is due to the presence of pigments (colored compounds). Two of these pigments, chlorophyll *a* ($C_{55}H_{72}O_5N_4Mg$) and chlorophyll *b*

($C_{55}H_{70}O_6N_4Mg$) are green; the other two, carotin ($C_{40}H_{56}$) and xanthophyll ($C_{40}H_{56}O_2$), are yellow.

Though not a component of chlorophyll, the element iron must be present in the plant for the formation of chlorophyll. The quantity and intensity of the green pigments largely mask the yellow pigments, although these do alter the color of the chloroplasts. It is the chloroplasts which give the color to the green cells of leaves and of the young parts of many stems. Organs which do not normally possess chloroplasts, such as the tubers of the potato, may develop green plastids when exposed to the light. In such cases leucoplasts which were present in the cells before exposure to light are stimulated to produce pigments and are thus transformed into chloroplasts.

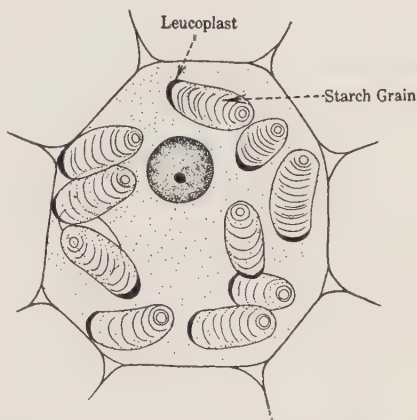


FIG. 10. — Starch-storing cell of *Pellionia* showing leucoplasts and starch grains. Note that starch grains are formed within the plastids. (Redrawn from Gager.)

The green plastids are the centers of the process of photosynthesis, by which the simple compounds, carbon dioxide and water, secured from the air and from the soil, are built up into sugar and starch. Leucoplasts are always present in cells in which starch is stored, such as those of starchy seeds, of the potato tuber, and of starch-storing roots like the sweet potato. They are able to change certain sugars (soluble carbohydrates) into starch. The starch is built up inside the leucoplasts into starch grains. As these grains increase in size the leucoplasts stretch to many times their original size.

Chromoplasts are responsible for the red, yellow, or orange color of many flowers and fruits. They owe their color prin-

cipally to the two pigments, carotin and xanthophyll. However, in many cases the color of flowers or fruits are due, not to pigments contained in plastids, but to colored substances dissolved in the solution contained in the vacuoles of the cells. A single plastid may be in turn a leucoplast, a chloroplast, and a chromoplast. This is the case in the cells of many fruits, such as the red pepper or tomato. In the young flower of these plants, the ovary, that part of the flower which develops later into the fruit, is almost colorless and the cells near the surface contain numerous leucoplasts. Later, the ovary, as well as the young fruit which develops from it, will become green; chloroplasts will be found to have developed from the leucoplasts. As the fruit ripens the chloroplasts are transformed to chromoplasts and the color of the fruit changes from green to red.

The Nucleus.—The nucleus is believed to control all the activities which go on in the living cell; its removal sooner or later results in the death of the cell. There is abundant evidence that it is material within the nucleus which is principally responsible for the fact that organisms inherit the characteristics of their ancestors. Typically the nucleus is a spherical structure, although ellipsoidal, disk-shaped, or considerably elongated nuclei often occur. It is surrounded by a definite **nuclear membrane** and contains a highly transparent watery or slightly jelly-like material called the **nuclear sap**.

Within the nuclear sap are the **nucleolus** (plural, **nucleoli**) and the **nuclear net**. The nucleolus is another cell structure concerning the function of which opinions differ. Usually the nucleus contains one nucleolus, but two or more may occur in a single nucleus, while in some cases they are lacking altogether. Nucleoli are generally spherical in form. At an early stage in the division of the nucleus at the time of cell division, nucleoli disappear entirely, but on completion of the process reappear in the two new nuclei.

The **nuclear net** is composed of granules scattered here and there along a network. The material of these granules is called

chromatin, and that of the network is called **linin**. Chromatin is without question a substance of very great importance. There is very conclusive evidence that it is this substance which bears the characteristics which the plant is able to pass on to successive generations. There can be no doubt that the resemblance of a plant to its parents is largely due to the fact that in the process of reproduction some of the chromatin of each parent plant is contributed to the new individual.

Inclusions.—The non-protoplasmic bodies which are called inclusions may be drops of liquid, or crystals, or solid bodies of various non-crystalline forms. They consist of (a) raw materials for food manufacture, (b) food or (c) by-products, and waste materials. While generally absent in very young cells, they soon appear and increase in number as cells grow older. Certain

kinds are particularly conspicuous in cells which serve for food storage. The commonest inclusions are the vacuoles, which are drops of liquid found in all but the very youngest cells. As the cell grows the vacuoles increase in size and some of them come into contact with each other and fuse. Thus they become fewer in number but larger in size in the older cells than in the younger ones. By the time the cell has reached its greatest size there is generally only a single large vacuole. Since this is commonly larger in volume than the protoplasm and occupies the

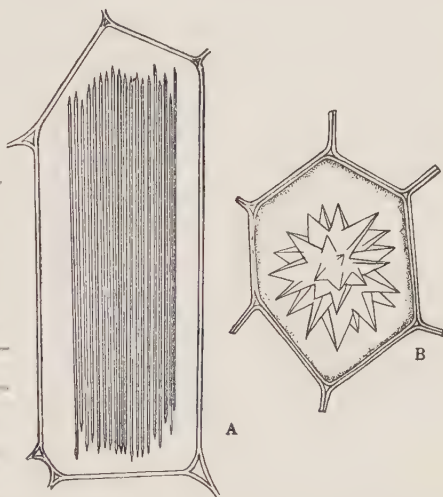


FIG. 11.—Crystal inclusions. A, a cell from the stem of spiderwort (*Tradescantia*) showing a group of raphides. B, a cell from the leaf-stalk of dock (*Rumex*) showing a cluster of crystals. In A the cytoplasm has been omitted.

center of the cell, the protoplast in old cells has the form of a closed sac. In such cells the nucleus lies near the cell wall, embedded in the cytoplasm, or is suspended in the large central vacuole by fine threads of cytoplasm which are connected with the cytoplasm lining the cell wall. In the latter case also the nucleus is surrounded by a layer of cytoplasm. It is never in direct contact with the vacuole or the cell wall.

The liquid within the vacuole is not pure water, but a solution of many substances dissolved in water. Among these substances are the gases of the atmosphere, including nitrogen, oxygen, and carbon dioxide; inorganic salts (such as nitrates, chlorides, sulphates, or phosphates of the metals potassium, sodium, calcium, or magnesium); organic acids (such as malic, formic, acetic, and oxalic acid), compounds of some of these acids with the metals named above; sugars (such as cane sugar and grape sugar); soluble proteins and simpler nitrogenous compounds; and other substances. The cell sap, as the content of the vacuole is called, is generally slightly acid. In many plants the cell sap contains dissolved anthocyanin pigments which give their flowers, leaves, etc., a red, purple or blue color. The common red beet owes its color to such pigments dissolved in the cell sap. In the carrot, on the other hand, the yellow color is due to pigments in the chromoplasts. In many flowers the two methods of coloration are combined.

In addition to vacuoles containing a watery cell sap, there are found in certain cells oil drops of considerable size which are sometimes spoken of as **oil vacuoles**. They never reach the size of the cell-sap vacuoles of mature cells.

Crystals.—Cells with crystal inclusions can be found in almost all plants. The crystals may be large ones occurring singly, numerous very fine ones scattered through the cytoplasm, bundles of fine sharp needles (**raphides**), or spherical groups of radiating crystals.

Starch Grains.—These inclusions are found in green cells after a period of active food manufacture, and occur regularly in

various food-storing cells such as those of the potato tuber and of many seeds. The stored starch of plants is the most important substance used as food by man. The starch grains which are produced in green food-making cells are formed within the chloroplasts. The grains of reserve starch consist of successive layers, which are often thicker on one side of the grain than on the other. This is conspicuously the case in the starch grains of potato. Sometimes a number of small grains are united into a group which is called a compound grain. Compound grains occur in rice, oats, and some other cereals. The starch molecule consists of carbon, hydrogen, and oxygen atoms united in the proportions of six of carbon to ten of hydrogen and five of oxygen. Starch grains are themselves insoluble in water, but are capable of conversion into certain sugars which are soluble.

When a green cell containing starch discontinues food manufacture, as it does when night comes on, the starch is changed into sugar and passes to parts of the plant where it will be used or stored. The sugar which reaches the storage organs may be stored in the cells in the form of sugar or may be converted again by leucoplasts into starch and remain in this form until it is needed by the plant. It is then changed back into sugar and passes to the part of the plant where it is to be used as food.

When starch grains are treated with a solution of iodine they become blue in color. The form of the grains of reserve starch is different in different plants, a fact which often makes it possible to determine, by microscopic examination of a sample of starch, from what kind of plant it was secured.

 **Absorption.**—*Solution.*—It is impossible for substances to enter the plant cell unless they are in solution in water. (Except where otherwise stated, the term solution, when used in this text, is to be understood as designating a **true** solution.) A true solution is a mixture in which the component particles are no larger than molecules. The gases of the atmosphere, oxygen and carbon dioxide, are absorbed by plants, but they must first go into solution in water before actually entering the cells. All

other substances are absorbed from the water solution in the soil. In many unicellular aquatic green plants, such as certain algae, all materials, including oxygen and carbon dioxide, are absorbed from the water (sea, stream, lake, pond) in which they are submerged. Soil water, sea water, and the waters of rivers, lakes, and ponds are generally very dilute solutions.

Diffusion.—This is a process which plays a very important part in the life processes of plants and animals. If a piece of some deeply colored soluble substance such as blue vitriol (copper sulphate) be dropped into a glass of water it will gradually go into solution. For some time, however, the solution will be more deeply colored in the vicinity of the solid fragment, indicating that the colored component of the solution is more concentrated (that is, the dissolved particles of solute are more crowded or nearer together) there than in more distant parts of the solution. In time the whole solution will become uniform in color, indicating that the dissolved particles of the solute have become uniformly distributed among the water particles.

Such scattering of the particles of one component of a solution among those of the other components, resulting in a uniform distribution of the particles of all components throughout the solution, is called **diffusion**.

Diffusion of solutes in liquids is not a rapid process and when we make a solution we do not ordinarily wait for diffusion to become complete, but hasten it by shaking or stirring.

Passage of Solvents through Membranes.—If water is carefully poured upon a quantity of sugar syrup (a concentrated solution of cane sugar and water) the two fluids will at first form two distinct layers. Soon, however, the molecules of water will diffuse into the concentrated sugar solution and those of the sugar will diffuse into the water, so that finally a uniform solution results. If the syrup and water are separated by a membrane like an ordinary cell wall through which the dissolved particles of sugar and water can pass freely, water will diffuse into the

syrup and sugar into the water so that the solutions on the two sides of the membrane will become equal in concentration. Such a membrane which permits water and all solutes to pass freely through it is called a **permeable membrane**.

There are membranes which permit water to pass freely, but restrict or prevent the passage of some or all solutes. Such a membrane is called a **semi-permeable membrane**.

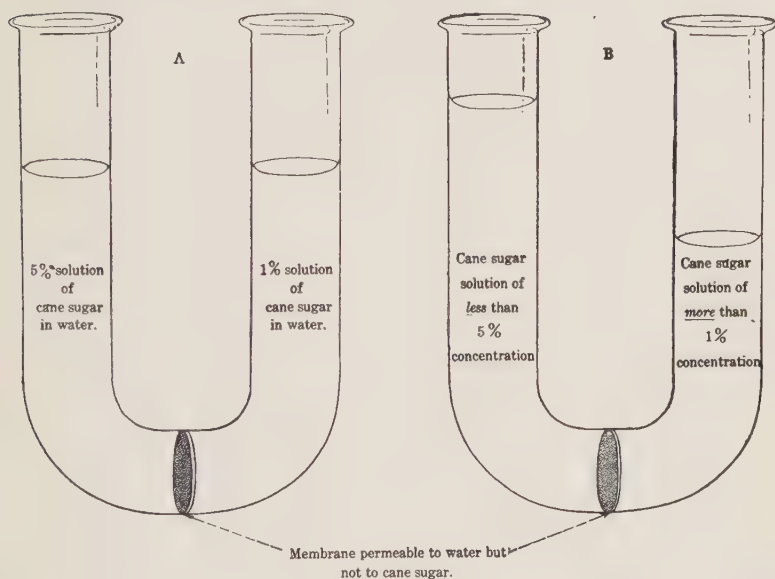


FIG. 12.—Diagram illustrating diffusion through a semi-permeable membrane.
For explanation see text, page 27.

When pure water or a dilute solution is separated from a concentrated solution by a semi-permeable membrane through which the solute cannot pass an interesting situation results. This will be easier to understand if we think of the membrane as stretched across the U-shaped tube shown in Fig. 12, *A* and *B*.

The left-hand arm of the tube in *A* is partly filled with a solution of 5 grams of cane sugar in 100 cubic centimeters of

water. The right-hand arm contains a dilute solution, say of 1 gram in 100 cubic centimeters of water. The level of the liquids in the two arms of the tube is the same and M is the membrane separating the two solutions. It is impermeable to cane sugar.

Now water diffuses from the more dilute solution on the right through the membrane to the more concentrated solution on the left.

The solute, cane sugar, tends on the other hand to diffuse from the more concentrated solution on the left of the membrane to the more dilute solution on the right. **The cane sugar will not pass, however, because the membrane is not permeable to it.** As a consequence of water passing through the membrane from right to left the following changes occur:

1. The volume of the solution in the right arm becomes less as the result of the loss of water. The concentration of the solution in the right arm becomes greater for the same reason.

2. The solution in the left arm becomes more dilute as the result of the addition of water from the other arm. Its volume becomes greater for the same reason.

3. The level of the solutions becomes different, as shown in B , the level rising in what was originally the more concentrated solution and falling in what was originally the more dilute.

The difference in level of the solutions in the two arms of the U-tube necessitates the conclusion that there is a pressure supporting the column which stands at the higher level. This pressure is called **osmotic pressure**.

It should be borne in mind that when two solutions are separated by a membrane the solvent will pass from one of the solutions to the other and give rise to osmotic pressure only if

- (1) the membrane is permeable to the solvent;
- (2) solutes are present which cannot pass freely through the membrane;
- (3) the number of dissolved particles of these solutes in a given volume of the solution is greater on one side of the membrane than on the other.

Diffusion of Solutes.—Figs. 12 and 13 illustrate the passage of the solvent through a semi-permeable membrane. Fig. 13 shows, in addition, the diffusion of one of the solutes. Most semi-permeable membranes permit the dissolved particles of some substances to pass freely but are relatively impermeable to those of other substances. The membrane separating the two solutions in Fig. 13 is such a **selective** membrane; it is permeable

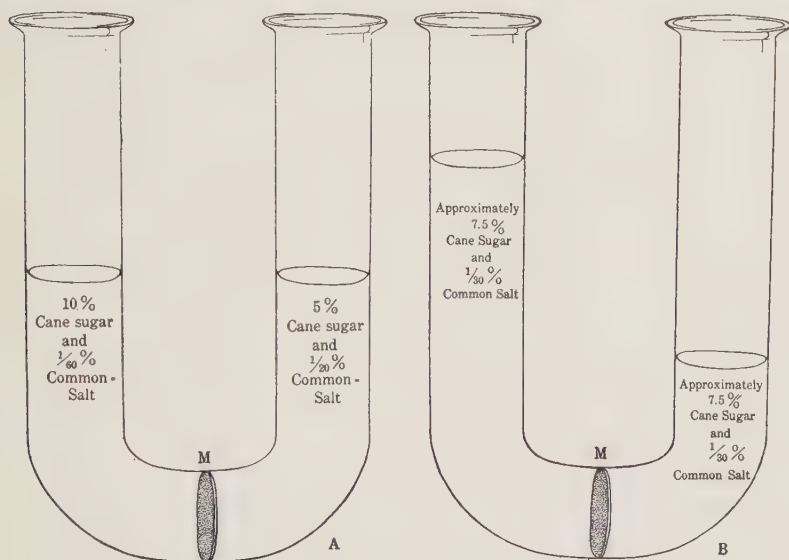


FIG. 13.—Diagram illustrating diffusion through a semi-permeable membrane. For explanation see text, page 29.

to water and to common salt, but not to cane sugar. As in the former examples, the result of diffusion is the establishment of relative uniformity of concentration in both arms of the U-tube. But whereas the salt content was equalized by the passage of salt particles from the arm where the salt was more concentrated to the arm where the salt concentration was less, equal distribution of the sugar was brought about by the passage of water from the arm where the concentration of sugar was less to the arm

where the concentration of sugar was greater, thus raising the level of what was originally the more concentrated solution. It should be noted that the movement of a particular solute is generally not affected by other solutes present.

Diffusion in Relation to (Absorption) by the Plant Cell.—The cellulose wall surrounding the protoplast is a permeable membrane and generally does not impede the passage, in and out, of any of the substances dissolved in the cell sap or in the water surrounding the cell. The cytoplasmic membrane, on the other hand, is semi-permeable. It freely admits the water and most of the substances dissolved in it from without the cell, but restricts the outward passage of most of the solutes in the cell sap. It also has the important property of changing its permeability, so that substances admitted at one time may be excluded at another.

The total concentration of dissolved substances is normally much greater in the cell sap than in the solution outside the cell. In the latter, however, certain substances will be present (dissolved) in greater quantity than in the cell sap. In the light of the foregoing explanations, the cell will therefore take up from without (*a*) water; and, since the behavior of a solute is independent of other solutes present, (*b*) certain needed substances.

The water taken in by the cell both enlarges the vacuole by increasing the cell sap and also permeates the protoplasm (which behaves as a colloidal solution) causing it to swell. Largely due to the former, a distending force known as **turgor pressure** is set up within the cell. So great is this pressure (reaching 20 kilograms per square centimeter in the sugar beet with its highly concentrated cell sap) that it would burst the protoplast were it not for the resistance afforded by the cell wall.

Every living plant cell, whether surrounded by other cells in a multicellular plant body, or existing as an individual unicellular plant immersed in the water of a pond, is normally in a state of such (fluctuating) turgidity. It will lose its turgor when placed in a solution more concentrated than its own cell sap. Some of

the water will then pass outward through the cytoplasmic membrane, the vacuole will shrink, and the cell will no longer be plump and distended. It is then said to be in a condition of **plasmolysis**.

In mastering these processes of absorption (and all other functions) of the cell, the student should guard against the error which often results from the necessity of each process being described and explained singly and separately. Just as a person,

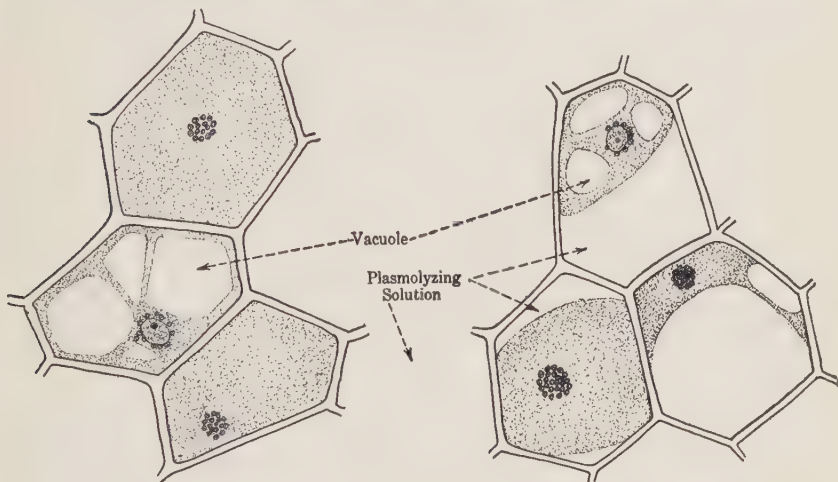


FIG. 14.—Plasmolysis of epidermal cells of the leaf of wandering Jew (*Zebrina pendula*). A, cells in water. B, cells after brief immersion in 20 per cent solution of cane sugar. Note that the spaces between the cytoplasm and the cell wall in the plasmolyzed cells are filled with the solution in which the cells are immersed.

In each drawing two cells are shown as seen in surface view and one in section.

while reading these words, may at the same time scratch his head and wriggle his toes, so in a cell (a living, functioning structure like himself) several processes may be going on simultaneously. Thus an absorbing cell, say one prolonged into a root hair, may at one and the same time be admitting water, taking in several different solutes at different rates, and giving out some solute.

☉ **Photosynthesis and Respiration.**—The energy needed by the cell for the performance of its functions—which means doing

work, is derived from the sun. When illuminated, under natural conditions by sunlight, all cells containing chlorophyll have the power of uniting water and carbon dioxide to form glucose. This is the process of **photosynthesis**. It will be treated more fully in connection with the physiology of the leaf.

The **solar energy** absorbed in photosynthesis is stored in the glucose as **chemical energy**. This is liberated when in the process of **respiration** the glucose or related substances produced from it are broken down again into water and carbon dioxide. As respiration requires no supply of energy from without, it can, and in fact, does go on continuously in all living cells.

These two processes are thus contrasted:

PHOTOSYNTHESIS

Its raw materials are carbon dioxide and water.

It goes on only in cells provided with chlorophyll.

It takes place only when the cells are illuminated, therefore, in nature only during the day.

It is an energy-absorbing process and continues only so long as light energy is supplied to the cell.

The energy absorbed is stored in the sugar molecule.

Its products are glucose, or other sugars, and oxygen.

The gas absorbed during photosynthesis is carbon dioxide, and that liberated is oxygen.

RESPIRATION

Its raw materials are glucose, other foods and oxygen.

It takes place in all living plant or animal cells.

It goes on at all times, by night as well as by day.

It is an energy-releasing process and is independent of energy sources outside the plant.

The stored energy of the sugar molecule is liberated in forms, such as heat energy, which are useful to the organism.

When the process goes on to completion its products are carbon dioxide and water.

During respiration oxygen is absorbed and carbon dioxide is liberated.

① **Assimilation.**—The conversion of carbohydrates, fats, proteins, and simpler nitrogenous foods into the living material (protoplasm) of the cell is called assimilation. It is a process

about which we can know very little until we understand much better than at present the nature of the protoplasm itself.

We shall use the term **food** only for those materials which are capable of yielding energy when respired and which may be utilized, without any considerable change, as building material for the protoplasm. For substances like water, carbon dioxide, and inorganic salts which the plant can utilize for the manufacture of foods but which cannot be respired, we shall use the expression, **raw materials for food manufacture**.

Growth.—Growth of the cell results in part from the increase in the quantity of protoplasm (by assimilation), and in part from a stretching of the cell wall due to turgor. During growth sugar is converted into cellulose by the protoplasm lining the cell wall. Thus the thickness of the cell wall also may be increased. The growth of a multicellular plant differs from that of a unicellular one in that it involves not only this increase in the size of cells and quantity of protoplasm but also increase in number of cells.

Multiplication of Cells.—After attaining a certain size the unicellular plant divides into two cells which then separate, and each after a period of growth repeats the process. In multicellular plants this power of repeated division is restricted to certain cells.

Cell division (*mitosis*) is a process in which there is a definite sequence of complex changes such as are shown in Fig. 15.

TISSUES

In multicellular plants, particularly the ferns and their allies and the seed plants, the plant body is made up of many different kinds of cells. Each kind of cell is adapted to serve a certain function in the life of the plant. Cells which are of similar structure and together perform a particular function constitute a **tissue**. The cells of the various tissues may differ in their form, in the thickness of their walls, in the length of life of the protoplasts, and in other particulars.

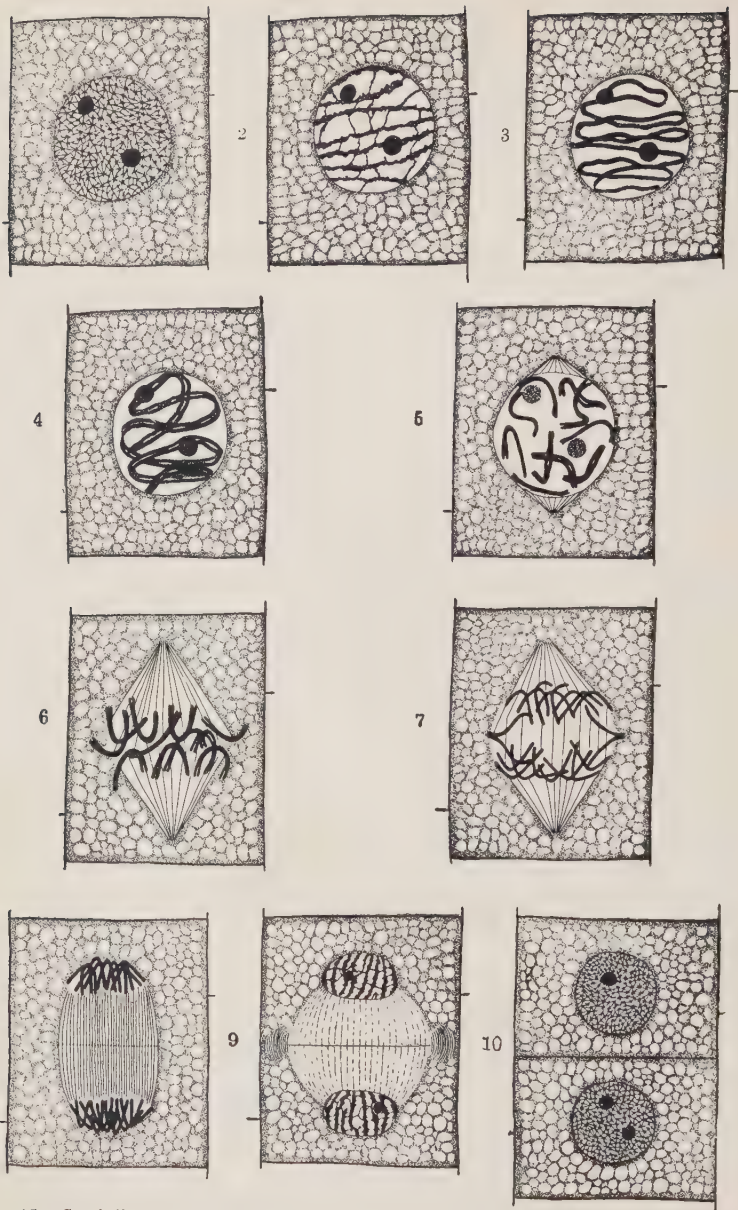


FIG. 15.—Semi-diagrammatic representation of a number of stages in the division of a cell of an onion root-tip. 1, resting nucleus. 2, formation of spireme thread from the nuclear net. 3, the formed spireme thread. 4, longitudinal splitting of the chromatin ribbon. 5, segmentation of the ribbon into chromosomes and beginning of spindle formation. 6, completion of spindle, disappearance of nuclear net and nucleoli, and arrangement of chromosomes at the equator of the spindle. 7, movement of daughter chromosomes toward the poles of the spindle. 8, the daughter chromosomes at the poles of the spindle, the spindle fibers thickening at the equator. 9, the daughter chromosomes reconstructing the nuclear net, reappearance of nucleoli and nuclear membranes, and cell-plate further advanced. 10, daughter cells in resting condition.

Meristematic Tissue.—At the tips of all the roots and branches of the plant are groups of cells which by repeated division give rise to new cells. The growth in length of the stem and root results from the formation of these cells and their subsequent elongation. Just outside of the cylinder of wood, which forms the greater part of the stem of a tree or shrub, is a single layer of cells which by their division continuously add to the wood and to the inner bark. This layer is called a **cambium**. Another cambium produces the outer bark of woody plants. These cambiums and the above-mentioned **growing points** at the tips of roots and stems are called **meristematic tissues**. The cells are thin-walled and seldom much longer than wide. The nucleus makes up a large part of the volume of the protoplast and the vacuoles are either absent or very small. Meristematic tissue is generally compact and without the intercellular spaces which characterize some tissues.

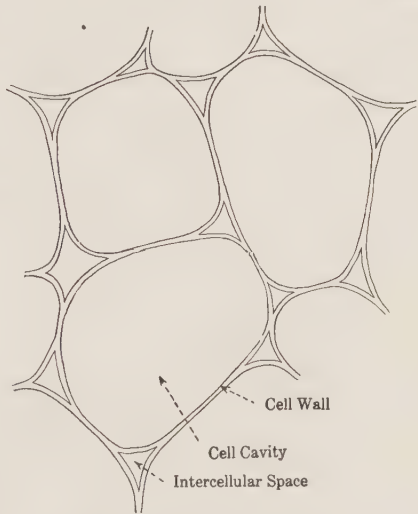


FIG. 16.—Typical parenchyma tissue. The cell contents are not shown.

Parenchyma Tissue.—Widely distributed throughout the plant are large isodiametric cells with thin cellulose walls, large vacuoles, and with air spaces between them (Fig. 16). Such air spaces are called **intercellular spaces**. The protoplasts of these cells remain alive for a long time. Cells of this type constitute a tissue called **parenchyma**. They resemble meristematic cells more closely than do the cells of any other tissue. The green parenchyma of leaves and young stems, which carries on photosynthesis, is often called **chlorenchyma**.

Epidermis (Fig. 17).—This is the tissue which forms the surface layer of all parts of ferns and flowering plants that are not covered with bark. Such a layer also occurs in some plants below the ferns. Except in the case of a very few plants, the epidermis is one cell thick and on the structures above ground consists of cells whose outer walls are thickened and convex. It is the outermost part of these walls which consists of **cutin**, a waxy substance highly impermeable to water and gases. This

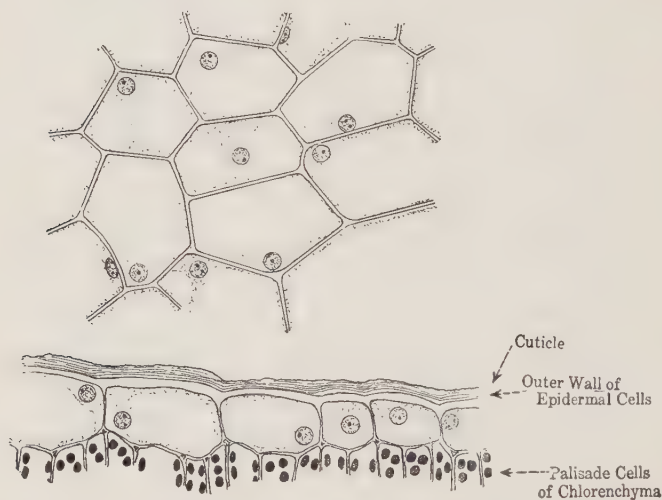


FIG. 17.—Ordinary epidermal cells from the upper side of a leaf. Above, surface view, below, as seen in section. For the stomata and guard cells see Figs. 79 and 80.

cutin forms a continuous layer or **cuticle** over all aerial parts lacking cork. Here the epidermis protects underlying tissues from drying out and to some extent from mechanical injury, whereas in the younger parts of roots it carries on absorption of water and soil solutes. The protoplasm in epidermal cells forms a thin layer lining the wall. Chloroplasts are generally absent from the epidermal cells except in the case of the special cells (**guard cells**) (Figs. 78, 79 and 80) which control the small openings (**stomata**) by which gases enter and pass out from the leaves

and young stems. The protoplasts of the epidermal cells are long-lived. From the thin-walled epidermal cells of the younger parts of the roots, tubular extensions (root hairs) closed at the ends, grow out into the soil. They are specially fitted to absorb water and inorganic salts from the soil. The structure and function of the root hairs are discussed in more detail on page 91.

Cork.—In the older parts of the stems and roots the epidermis is replaced by many layers of a tissue called cork (Fig. 18). This forms the outer bark of trees.

(It is from this outer bark of the cork oak (*Quercus suber*) that the cork of commerce is secured.) The cork cells are generally flattened, and have relatively thin walls and no intercellular spaces. Between the middle lamella and the inner cellulose layer of each of these cells is a layer of **suberin**, which renders the cells almost impermeable to water or gases and makes this tissue an excellent protection against excessive loss of water and against mechanical injury. The protoplasts of cork cells die very soon after the cells are formed.



FIG. 18.—Cork cells from the stem of Dutchman's pipe (*Aristolochia*).

Mechanical Tissue.—In typical plants different kinds of cells are so differentiated and arranged in the plant body as to give greater mechanical strength than can be secured merely by the high turgidity of the living cells. These cells constitute the strengthening or mechanical tissues. They have their walls thickened entirely or in part. The principal mechanical tissues are **collenchyma**, **bast fibers**, **wood fibers** and **stone cells**.

Collenchyma.—The cells of this tissue are elongated and thickened at the corners. The protoplasts are long-lived and chloroplasts are frequently present. Collenchyma (Fig. 19) is

the first of the mechanical tissues to be developed and therefore is found even in the young parts of the stem. Its cells are capable of considerable elongation after they are formed. The walls are of pure cellulose.

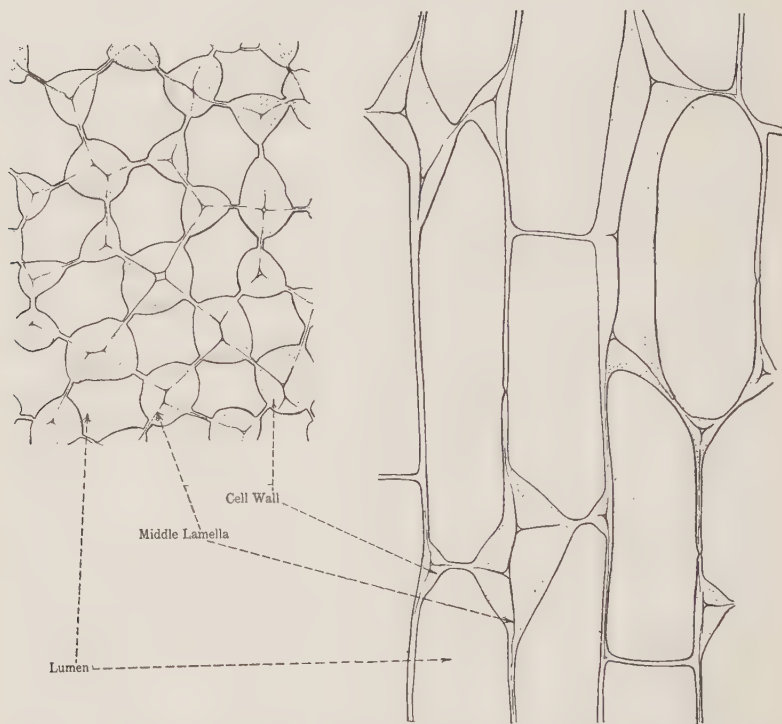


FIG. 19.—Collenchyma tissue. (Left), cross section. (Right), longitudinal section. The cell contents are not shown.

Fibers.—These are elongated, thick-walled cells, generally pointed at the ends. In extreme cases they may be as long as 10 inches. Soon after the fibers have attained their full size and thickness of walls the protoplasts die. The walls of these cells generally undergo lignification, that is, a part of their cellulose is modified into **lignin**. This results in an increase in strength and hardness but does not decrease their permeability

to water and dissolved substances. Fibers are very elastic and can be stretched to a remarkable degree without losing the power to return to their original length. According to their location, outside or inside the cambium ring, they are called either **bast** fibers or **wood** fibers. They are the most important mechanical elements in the plant.

Stone Cells.—These are cells with walls much thickened and lignified like the fibers, but differing from them in not being greatly elongated.

Conducting Tissue.—There are three kinds of structures especially adapted for conduction of materials from one part of the plant to another: **tracheids, tracheal tubes, and sieve tubes.**

Tracheids.—These are single dead cells, always elongated, and generally pointed at the ends (Fig. 20). The walls are thin in certain places and thick in others. Sometimes the thickening is restricted to rings or spiral bands running around the cells. In other cases the entire wall is thickened except for numerous small, round, or oval areas or pits (Fig. 34). The walls of tracheids are always lignified.

Tracheal Tubes.—A tracheal tube is not a single cell but a tube made up of a series of somewhat elongated, cylindrical cells with most of the end walls dissolved away. Functional tracheal tubes have no living contents, as the protoplasm of the component cells dies. These tubes, like the tracheids, have parts of their walls thickened. In a part of the stem which has not yet finished growth in length there are thickened rings or spirals. Those which are formed later have the wall much more completely thickened, the thin areas forming pits of various shapes. The walls, as in tracheids, are always lignified. Tracheal tubes are often several centimeters in length (distance between two successive cross walls) and in some trees may exceed a meter.

Sieve Tubes.—These are vertical rows of elongated cells the oblique end walls of which are thickened, and provided with pits (Fig. 21). Pitted areas also sometimes are present in the lateral walls. Through these conspicuous perforations (whence

the name sieve tubes) pass cytoplasmic strands connecting the cytoplasm of adjoining cells.

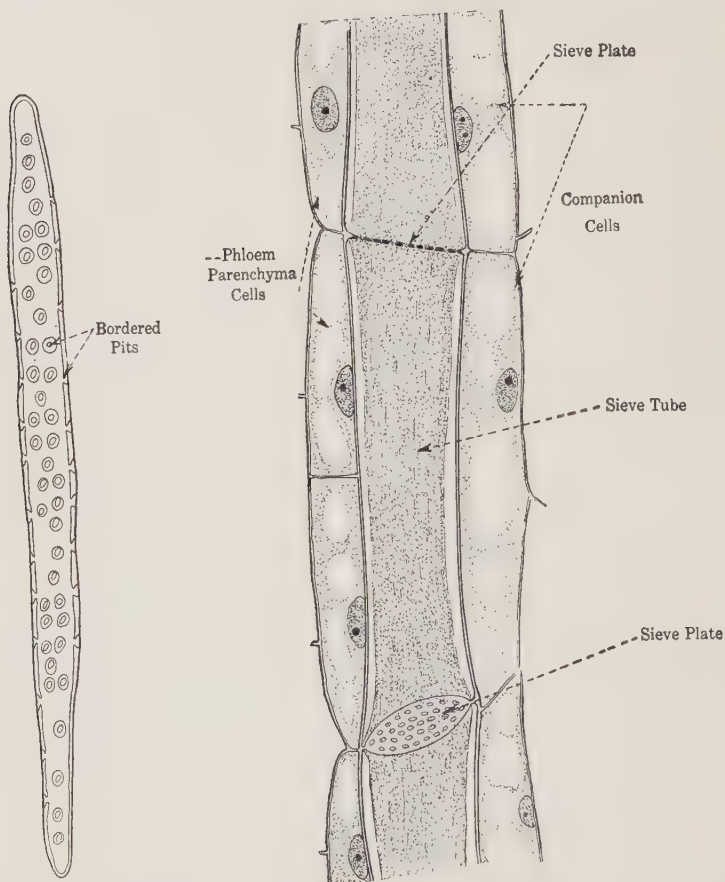


FIG. 20.—A single pitted tracheid from pine (*Pinus*) wood

FIG. 21.—A sieve tube and companion cells from the stem of squash (*Cucurbita maxima*).

The cytoplasm of the sieve tubes consists of a thin layer surrounding a large central vacuole. In some cases nuclei are lacking. At the time of the formation of a sieve tube, an adjacent

row of **companion cells** is produced. Though these cells equal in length those composing the sieve tubes, they present a striking contrast by virtue of their small cross section and dense cytoplasm. The walls of both companion cells and sieve tubes are of cellulose. Those separating the companion cells from the sieve tubes are always pitted.

Proteins and simpler nitrogenous organic compounds are abundant in the sieve tubes, and it is probable that the principal function of the tubes is the conduction of such substances. Proteins, which even in solution pass with difficulty through cell walls, are able to pass freely through the pores of the end walls (**sieve plates**) of these tubes. In many cases a deposit, called **callus**, is formed over the sieve plates and closes the pores. The callus masses are composed of a carbohydrate, **callose**.

CHAPTER III

THE STEM

THE reader will recall that the plant body of a typical seed plant consists of the major divisions, root and shoot, and that the latter in turn is composed of two kinds of organs, namely, the leaf and the stem. It is the stem with which we are concerned at present.

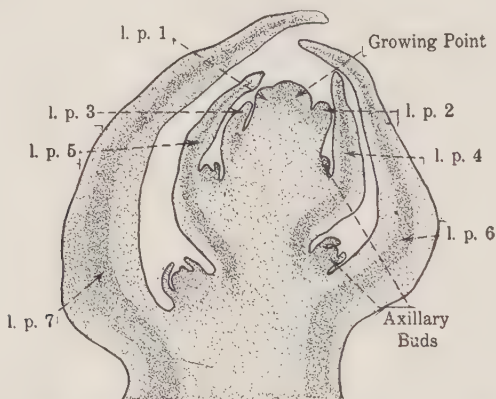


FIG. 22.—Longitudinal section of terminal bud of Dutchman's pipe (*Aristolochia*). The leaf primordia are numbered in the reverse order of their formation, l. p. 1 being the youngest and l. p. 7, the oldest of those shown.

The entire stem systems of most plants grow in air, but in some plants, such as most common ferns, the stem system is under ground, and in other plants, such as *Elodea*, *Potamogeton*, and water lilies, the medium of growth of the stems is water. Asparagus, rhubarb, and Irish potatoes produce both aerial and subterranean stems.

Origin of the Stem.—In most species of seed-bearing plants (Spermatophyta) each individual arises from a seed, which con-

sists of a rudimentary plant called the embryo, with a store of food and protective coats. The embryo plant has at one end a rudimentary root from which the whole root system of the adult plant may develop and at the other a plumule which develops



FIG. 23.—Three twigs of ash (*Fraxinus*) showing the opening of the terminal bud. The bud to the left is swelling but the bud scales have not yet separated. The bud scales of the second bud have separated but as yet the internodes and rudimentary leaves within the bud have grown very little. The picture to the right shows the bud fully opened and leaves and internodes well advanced in development.

into the shoot. At the center of the plumule is a cone-shaped mass of meristematic tissue which by the division of its cells makes possible the growth of the stem of the seedling plant. It is this stem which generally continues as the main stem of the

adult. In plants which have developed from seeds the origin of the stem is, then, in the terminal bud or plumule of the embryo. In all other cases the stem originates in a bud present upon a stem cutting or developed upon either root cuttings or detached leaves. Every branch stem originates also in a bud.



FIG. 24.—Five twigs of buckeye (*Aesculus*) showing successive stages in the opening of the terminal bud and in the growth of the internodes and leaves which, in a rudimentary condition, were contained within the bud. All the parts above the dotted line belonged to the terminal bud or were developed from it within a period of three weeks from a terminal bud like the one shown at the extreme left. A decimeter scale is shown at the bottom of the figure.

Growth and Development of Stems.—The growth in length of a stem would not be possible without the addition of new cells by the meristematic tissue of the growing point in the terminal bud. Nevertheless, it is not at the growing point but some distance behind it that most active elongation of the stem takes place. Passing downward from the very tip of the stem, four growth regions or zones may be recognized: (1) a region of meristematic activity with slight growth in length, (2) a region of

active elongation, (3) a region of differentiation of tissues in which there is little elongation, and (4) a mature region, making up the rest of the stem, in which there is no elongation. The first region includes most of that part of the stem which is within the bud. It is generally several nodes and internodes in length. The region of active elongation extends from the base of the bud downward through several more nodes and internodes. The rapid growth in length in this region is due to the relatively short and little vacuolated cells of the first region becoming greatly vacuolated, taking up large quantities of water, and stretching lengthwise as a result of the high turgor. Growth in length of the stem is due principally to the elongation of successive internodes rather than to growth of the nodes.

In most herbaceous plants and in many tropical and subtropical woody plants this continues throughout the whole season of vegetative activity, whereas in many woody plants of the temperate and colder regions, most of the elongation of the stem is crowded into a few weeks of early spring.

STRUCTURE OF STEMS

Although stems vary considerably, due to differences in kinds of tissues and their arrangement, the following principal types will illustrate the structure and development of the stems of most seed bearing plants (Spermatophyta): (1) the **woody dicotyledon-gymnosperm**, (2) the **herbaceous dicotyledon**, and (3) the **monocotyledon**.

Before describing these types it will be necessary to distinguish between the principal groups of seed plants referred to in the above classification.

The Spermatophyta are divided into two classes, the Gymnospermae and the Angiospermae. The Gymnospermae (naked-seeded plants), are usually woody evergreens with needle- or scale-like leaves, as illustrated by the pines (*Pinus*), spruces (*Picea*), firs (*Abies*), and redwoods (*Sequoia*). In the vast majority

of cases they bear their seeds exposed, generally on the surface of a cone scale.

The *Angiospermae* (covered-seeded plants) are generally broad-leaved, and bear their seeds in closed structures known as fruits, such as a pea pod, an acorn, or an apple.

The *Angiospermae* consist of two subclasses, the *Dicotyledonae* and the *Monocotyledonae*. The first of these contains many more species than the second. The grasses, which include the cereals, the lilies, the palms and the orchids, are among the principal families of the monocotyledons. Most other common angiosperms are dicotyledons. A large number of those dicotyledons which live for several years are deciduous, losing their leaves once each year and later producing new leaves. In this respect they are in striking contrast with the evergreen gymnosperms.

THE WOODY DICOTYLEDON-GYMNOSPERM TYPE OF STEM

Gross Features of Structure.—Upon examination of the cut end of a stem a few centimeters in diameter several regions can

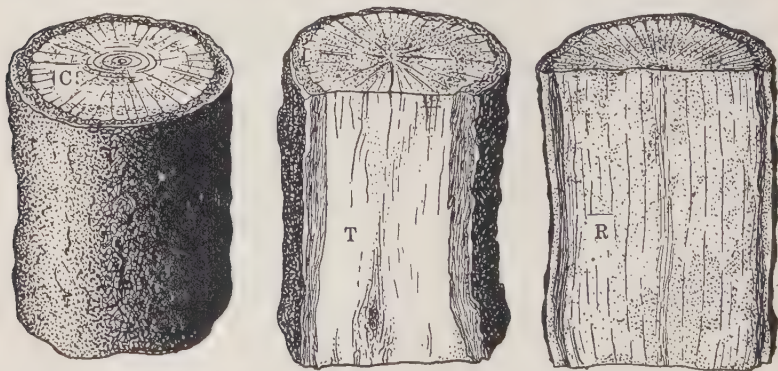


FIG. 25.—Stems showing three kinds of sections: *C*, cross or transverse. *T*, tangential. *R*, radial.

be distinguished. Of greatest extent is the central cylinder of **wood**. The **bark**, which includes the tissues outside of the woody

cylinder, may easily be removed from this, because of the layer of thin-walled, easily broken cells, the vascular **cambium**, lying next to the wood.



FIG. 26.—Cross section of a redwood (*Sequoia sempervirens*) log showing annual rings, light-colored sapwood, and dark-colored heartwood. Note the radial splitting which gives evidence of greater tangential than radial shrinkage of the cells during drying. (From Division of Forestry, College of Agriculture, of the University of California.)

Somewhat closer examination of the woody cylinder shows at the center the **pith**, which consists of softer tissue. Between

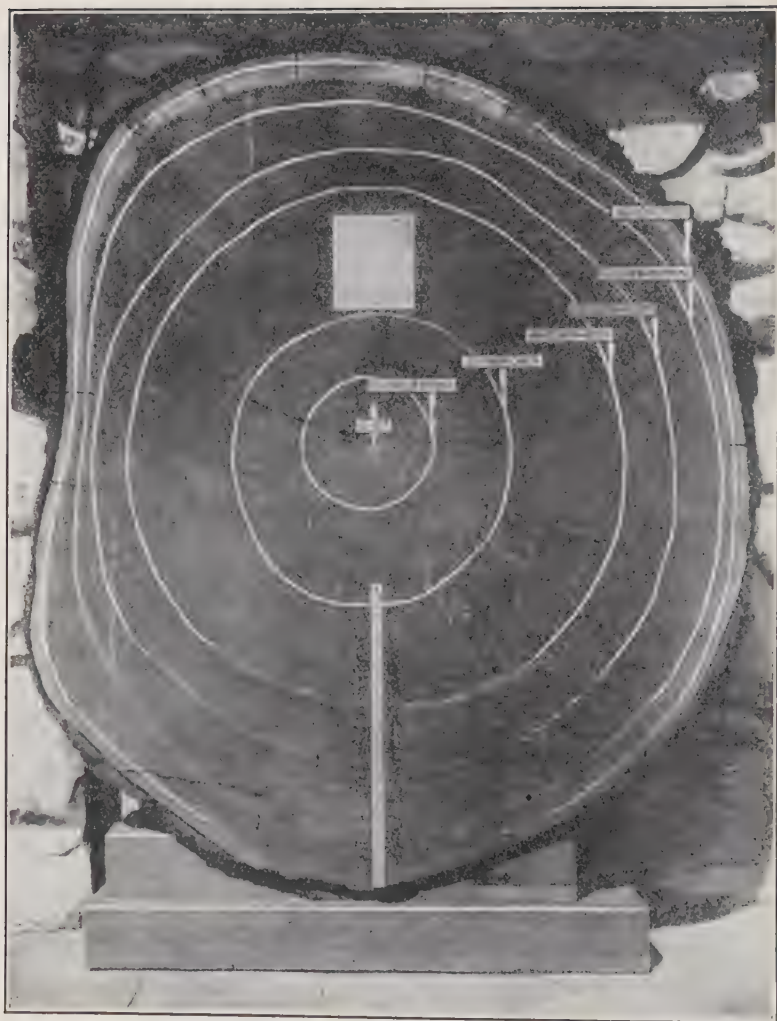


FIG. 27.—A cross section of the trunk of a relatively young tree of *Siquoia gigantea* (Big tree). The chalk lines and the arrows, except the central one, indicate the approximate location of the annual rings formed in the years during which a number of events of great historic importance took place. The tree from which the section was cut began its growth in about A.D. 923 and was about 1000 years old when cut. There are trees now standing which are certainly twice that age and probably living trees exist which are 3000 years old.

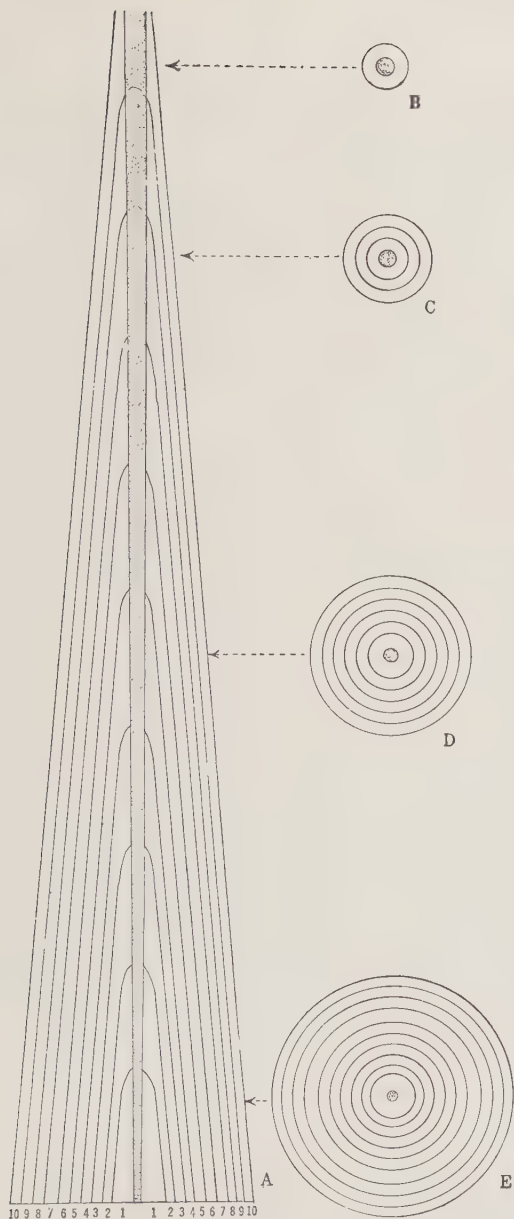


FIG. 28.—Diagrams of longitudinal and cross sections of a ten-year-old tree. Note the decrease in the number of annual rings from the base of the trunk to the apex.

the pith and the cambium and concentric with both are a number of circular lines. The tissue between one of these lines and the next is an **annual ring**, and consists of the cells added to the wood by the cambium in a single year. The number of annual rings seen in cross section of a tree generally indicates the age of the trunk at that height. The radiating lines of varying length in the wood are the **wood rays**.

The Origin and Development of the Tissues.—The development of the tissues can best be understood by examining a series of transverse sections through the stem from the growing point downward. It should be constantly borne in mind that the greater the distance any portion of the stem is from the growing point the older it is.

The Stem at the Growing Point.—The meristematic cells of the growing point constitute a tissue known as the promeristem. Meristematic cells are essentially alike. They are small cells lacking intercellular spaces and having thin cellulose walls, relatively large nuclei, and dense cytoplasm; they are without vacuoles, and have the capacity for repeated division.

The Stem a Short Distance Back of the Growing Point (Fig. 29).—Just back of the growing point, the cells from the promeristem have differentiated somewhat in size and shape to form three main tissue groups: the **protoderm**, the **ground meristem**, and the **procambium strands**. These three are **primary meristems**. These cells continue to divide though less actively than those of the promeristem. By further differentiation they give rise to the **primary permanent tissues** which are tissues no longer capable of active cell division but fitted to carry on the various activities of the stem.

The protoderm is the outermost layer of cells. It develops into the **epidermis**, a primary permanent tissue.

The ground meristem makes up the greater part of the tissue within the protoderm. It consists of relatively large thin-walled isodiametric cells, among which there may be intercellular spaces. It differentiates into the following primary permanent tissue

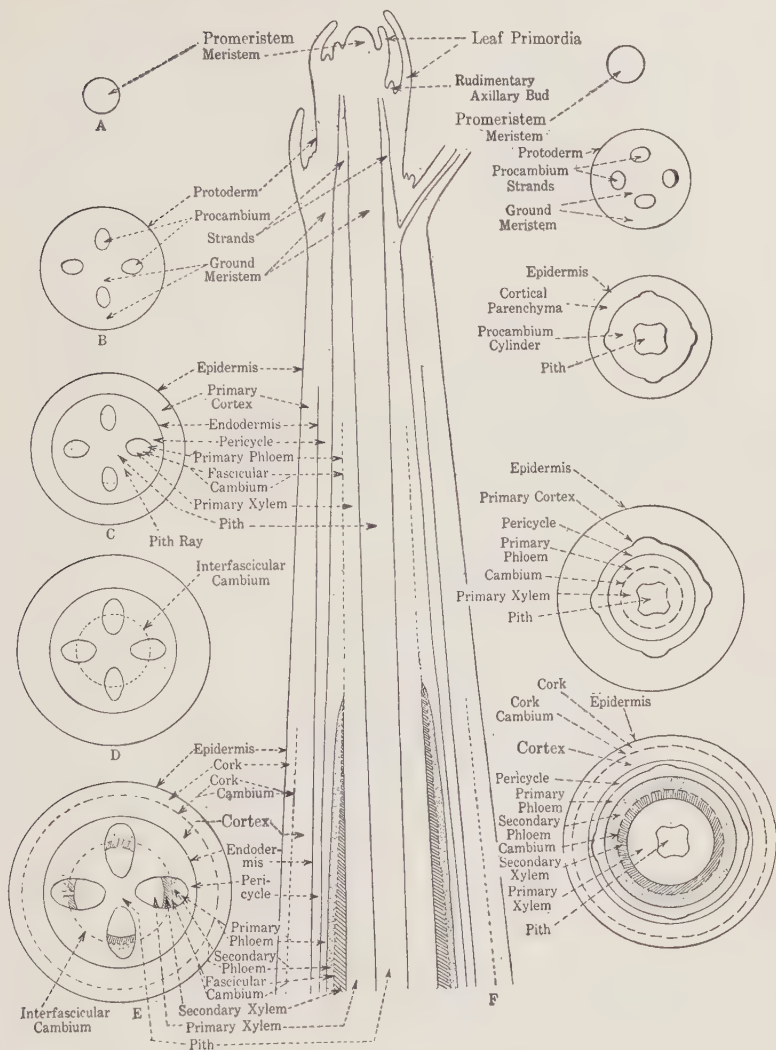


FIG. 29.—Diagram of longitudinal and cross sections of typical dicotyledonous stems; showing primary and secondary growth. On the left, cross sections of stem having distinct procambium strands and separate vascular bundles. On the right, sections of a stem with procambium cylinder and vascular cylinder.

groups: the **primary cortex**, the **pericycle**, the **pith rays**, if these are present, and the **pith**.

When procambium cells first become distinguishable from the promeristem they are generally in strands, therefore appearing in a transverse section as isolated groups of cells. These strands are arranged in a circle. A little later more procambium cells may be formed between these strands until in many stems there is produced a continuous hollow cylinder (a ring in cross section) of procambium. In some stems the strands never join in this way. From the procambium three tissue groups or regions are derived as differentiation goes on. (See Fig. 29.) These are the **phloem**, the **cambium** and the **xylem**. In the cases where the procambium strands do not join to form a **procambium cylinder** the phloem, xylem and cambium form single strands constituting **vascular bundles** (see Figs. 33 and 47), and the **cambium** is spoken of as **fascicular cambium** (cambium belonging to a bundle).

The One-year-old Stem.—During the first season's growth of the stem, differentiation of the primary permanent tissues from the primary meristems is completed. These primary permanent tissues constitute the following tissue groups: (1) the epidermis, (2) the primary cortex, and (3) the stele, including (a) the pericycle, (b) the vascular tissue, (c) the pith rays if they be present, and (d) the pith or medulla.

The Epidermis.—This usually is a single layer, the cells of which are generally isodiametric as seen in transverse section but somewhat elongated in the direction of the stem's length. Due to the cuticle and the thickening of the outer walls of the cells, the epidermis protects the aerial plant parts from excessive water loss, from mechanical injury, and from attacks of insects and fungi.

The Primary Cortex.—The primary cortex is one of the regions differentiated from the ground meristem. This tissue group is bounded externally by the epidermis and internally by the pericycle. The outer cells of the cortex, those lying just

beneath the epidermis, are usually **collenchyma**, a type which constitutes the first mechanical or strengthening tissue of the developing stem.

Beneath the collenchyma is a zone composed chiefly of thin-walled parenchyma. It is this zone which makes up the larger part of the primary cortex. Both the collenchyma and paren-

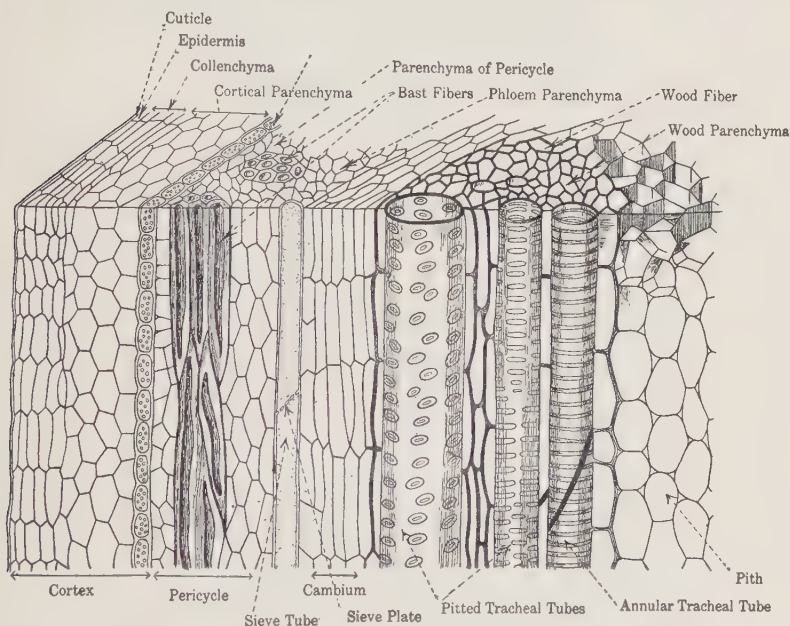


FIG. 30.—Diagram showing portion of a dicotyledonous stem in cross and radial sections. (Redrawn from Kerner.)

chyma cells of the cortex usually possess chloroplasts and consequently have the power of photosynthesis.

The Pericycle.—Lying beneath the cortex is the pericycle, a region which extends inward to the phloem. The pericycle is usually composed of two kinds of tissue, sclerenchyma and parenchyma. The sclerenchyma of the pericycle is made up of closely fitting fibers which may occur in isolated groups opposite the vascular bundles or form a continuous ring. The parenchyma

cells of the pericycle, like those of the cortex, may contain chloroplasts and carry on photosynthesis.

The Pith and Pith Rays.—The pith is made up of large-celled parenchyma with relatively numerous intercellular spaces. Its principal function in woody stems is food storage. In stems in which the vascular tissue does not form a continuous hollow cylinder, the bundles are separated by pith rays, wide strips of parenchyma extending from the pith to the pericycle.

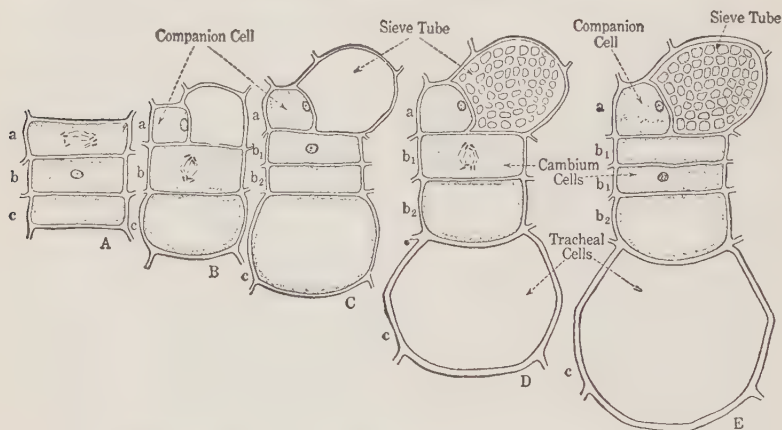


FIG. 31.—Diagrams showing the differentiation of daughter cells of the cambium. In A, B, C and D the cell marked *b* or *b'* is the cambium cell. Diagrammatic.

The Vascular Tissue.—The procambium cells on the outer side of the strand or cylinder become transformed into phloem and on the inside, into xylem. Some of the procambium cells lying between the xylem and phloem do not differentiate but, as a cambium layer, continue to function as meristematic cells.

The Phloem.—The phloem of dicotyledonous stems consists of three kinds of tissue elements: sieve tubes, companion cells, and phloem parenchyma cells. Sometimes fibers also are present. Sieve tubes and companion cells have already been described in the chapter on The Cell (see page 39). The phloem of gymnosperm

stems is essentially the same as that of woody dicotyledons except that companion cells are lacking.

The Cambium.—This is a single layer of cells lying between the xylem and the phloem which remain undifferentiated and

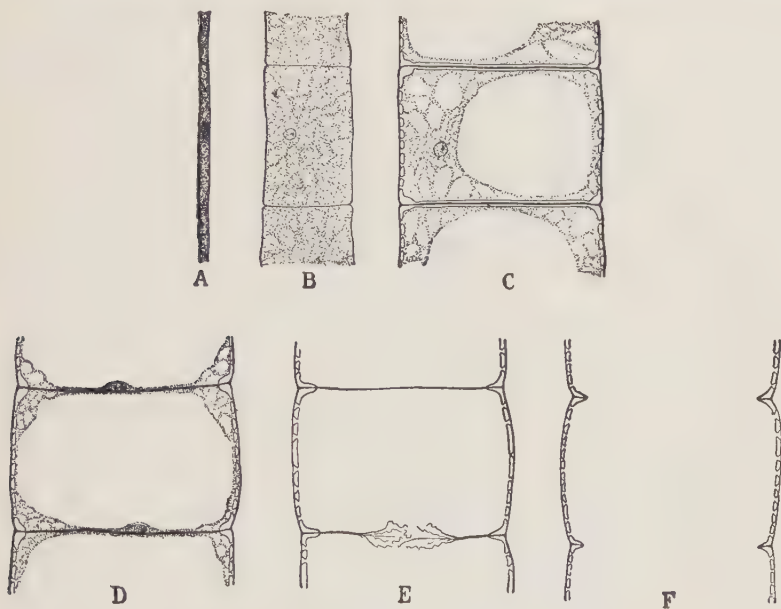


FIG. 32.—Development of a tracheal tube segment in *Robinia pseudacacia*. A, daughter cell of cambium which is to develop into a tracheal tube segment. B, the cell much enlarged. C, the cell still further enlarged, the secondary wall well developed. D, the cytoplasm restricted to the periphery, the nucleus adjacent to the wall where dissolution is occurring. E, the cytoplasm lost, the very thin end walls disintegrating. F, the mature, perforated empty cell. (From Eames and MacDaniels, *An Introduction to Plant Anatomy*, McGraw-Hill Book Company.)

retain the power of division, that is, remain meristematic. It is made up of small, thin-walled cells flattened tangentially, rich in protoplasm, and capable of repeated division. The cambium by its division gives rise to new phloem and xylem and thus causes the stem to increase in thickness.

Xylem (Wood).—The principal structural elements which compose the xylem, or wood, of one-year-old dicotyledonous stems are: tracheal tubes, tracheids, and wood parenchyma. Tracheal tubes are absent from the wood of gymnosperms. For a descrip-

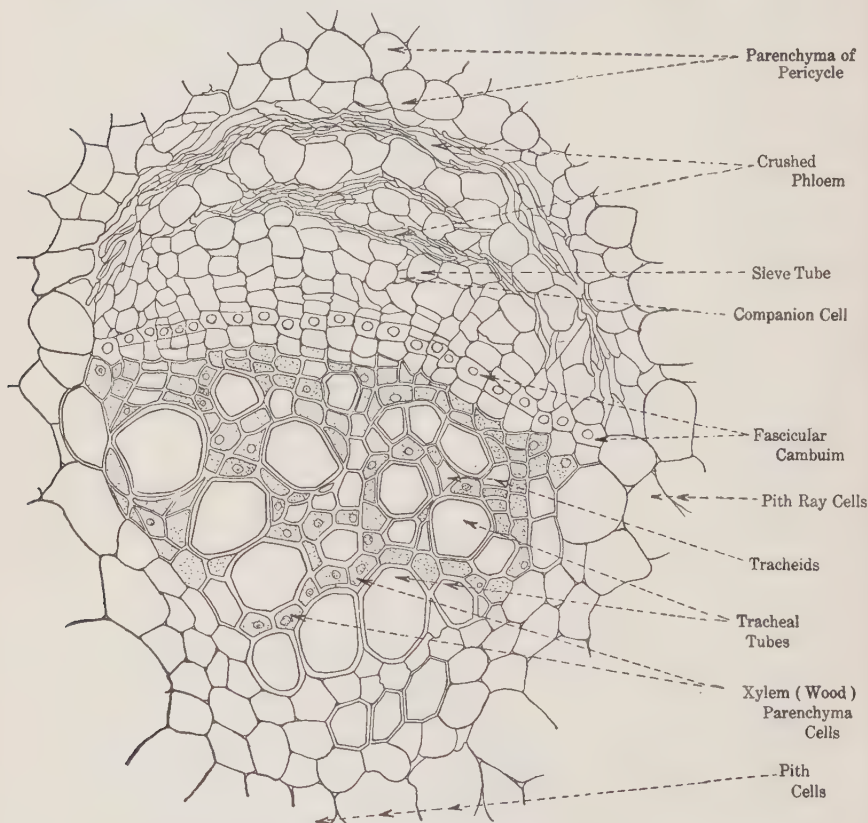


FIG. 33.—Cross section of a young vascular bundle of a dicotyledonous stem. (*Aristolochia*.)

tion of tracheal tubes and tracheids see the chapter on The Cell, page 39. Wood parenchyma cells are short, thin-walled and often pitted. Their protoplasts remain alive long after those of the tracheal tubes, tracheids and wood fibers are dead.

Secondary Growth in the Woody Dicotyledon-Gymnosperm Stem.—

The changes from promeristem to the primary permanent tissues are spoken of as the primary growth of the stem. This growth ends when all the tissues have differentiated except the cambium, which remains meristematic throughout the life of the stem. By the time the primary growth has been completed, normally within a few months, the part of the stem in question has generally ceased elongating. (Following this there is a secondary growth, resulting in an increase in thickness, which may continue for hundreds of years, or even several thousand in the sequoias.) Secondary growth results from the production of new cells by two lateral meristems, the **vascular cambium**, which has already been mentioned, and the **phellogen**, or cork cambium.

The Cambium Ring.—In stems with the vascular tissue in a continuous cylinder the vascular cambium is at this time already in the form of a continuous ring.

In those having separate vascular bundles, the cambium is interrupted by the pith rays. In such cases certain pith ray cells lying between the cambium of adjoining bundles undergo cell division, giving rise



FIG. 34.—Diagram of a portion of the wall of a tracheid of *Pinus* showing the structure of bordered pits. Above and to the left a pit is shown in section. It is the commonly accepted opinion that these pits provide a means for easy passage of sap through the thin wall of the pit without danger of perforation of the wall under high pressure. This latter end seems to be served by the thickened portion (torus) of the pit membrane. Under pressure it is forced against the opening in the border of the pit and relieves the strain on the thin portion of the pit membrane.

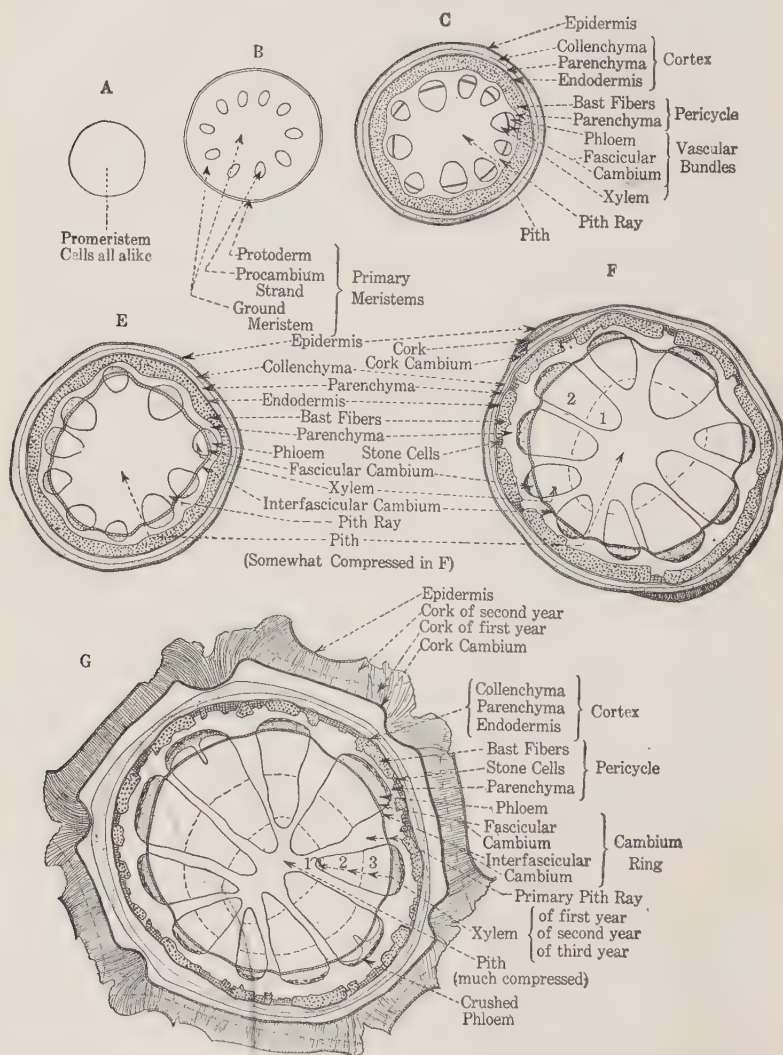


FIG. 35.—Diagrams showing primary and secondary growth of the stem of dicotyledon (*Aristolochia*) having separate vascular bundles.

to a row of rectangular meristematic cells similar to those of the bundle cambium, and known as **interfascicular cambium** (Fig. 36). Thus there is formed in these stems also a continuous vascular cambium ring.

The cambium ring generally consists of a single layer of meristematic cells, which by their repeated tangential divisions give rise

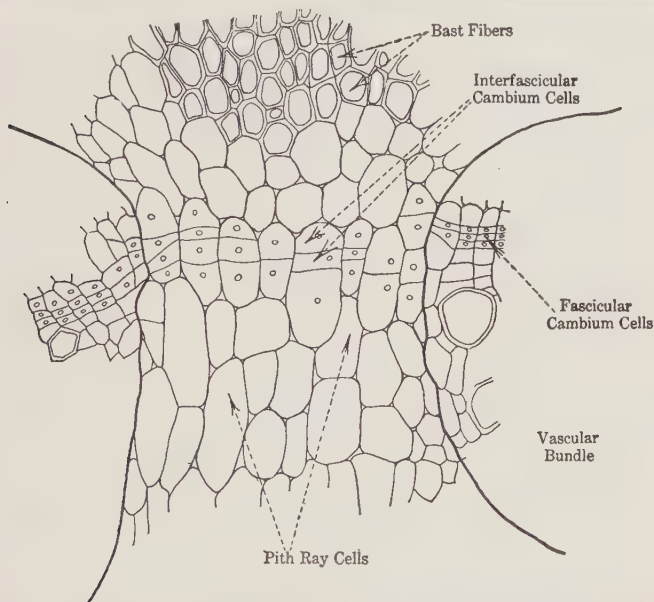


FIG. 36.—Part of a pith ray and of two vascular bundles of a young *Aristolochia* stem, showing the origin of interfascicular cambium cells from pith ray cells.

to new xylem and phloem elements (Figs. 31 and 32). When a new xylem element is to be formed, a cambium cell divides tangentially into two daughter cells. As a rule the inner daughter cell, which is the one next to the xylem, develops into a xylem element, and the outer daughter cell, next to the phloem, remains a cambium cell. Then this cell, which has remained cambium, again divides and, as before, the outer daughter cell retains its power of division. Less frequently when a cambium cell divides

into two daughter cells, the outer daughter cell, which is the one next to the phloem, develops into a phloem element and the inner daughter cell remains meristematic. This process is repeated throughout the growing season. Thus by division of the cells of the cambium ring, new xylem is added on the **outside** of the old xylem, and new phloem is added on the **inside** of the previously formed phloem.

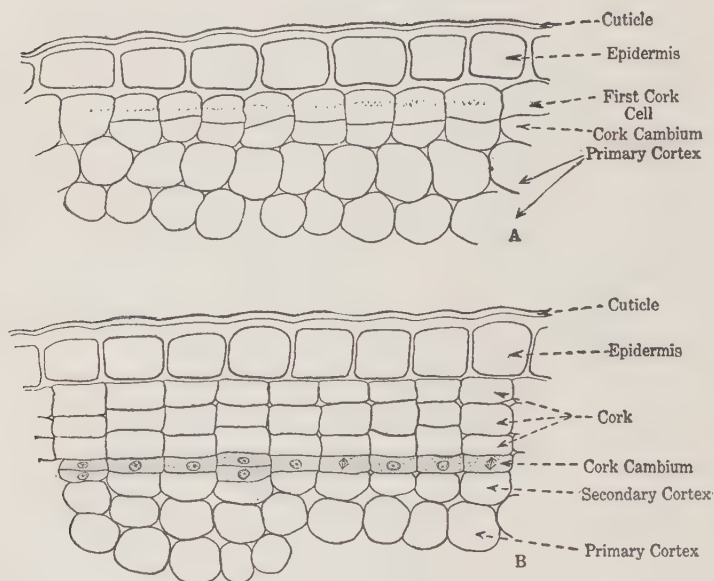


FIG. 37.—Cross sections of portions of a stem showing origin of cork cambium (A), and the development of cork and secondary cortex from cork cambium (B).

As the width of the xylem (from vascular cambium to pith) increases, the distance between the phloem and the inner xylem becomes greater. There is presumably, as a result, need for better conduction of water radially from the xylem to the phloem and of food from the phloem to the xylem. This need is met by the production of **vascular rays** by the cambium. Here and there a longitudinal row of cambium cells or several adjoining rows cease

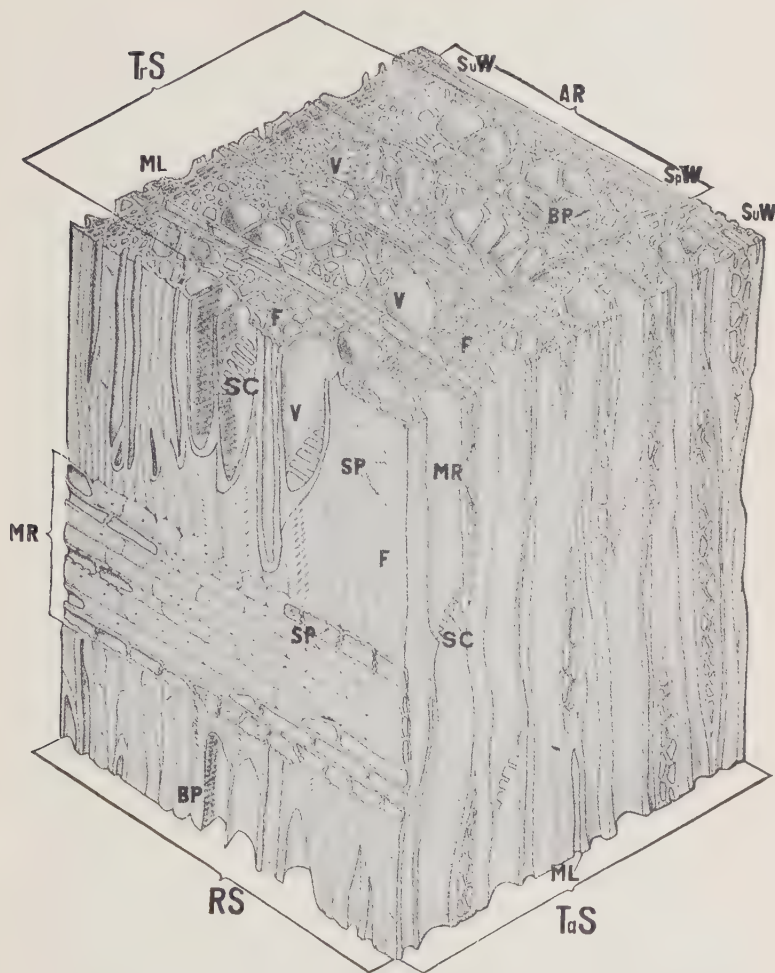


FIG. 38.—Diagram of a typical hardwood. *TrS*, cross section; *RS*, radial section; *TaS*, tangential section; *AR*, annual ring; *SuW*, summer wood; *SpW*, spring wood; *MR*, xylem ray; *V*, vessel; *F*, wood fiber; *SP*, simple pits; *BP*, bordered pits; *SC*, scleriform perforations; *ML*, middle lamella. (After chart by U. S. Forest Products Laboratory.)

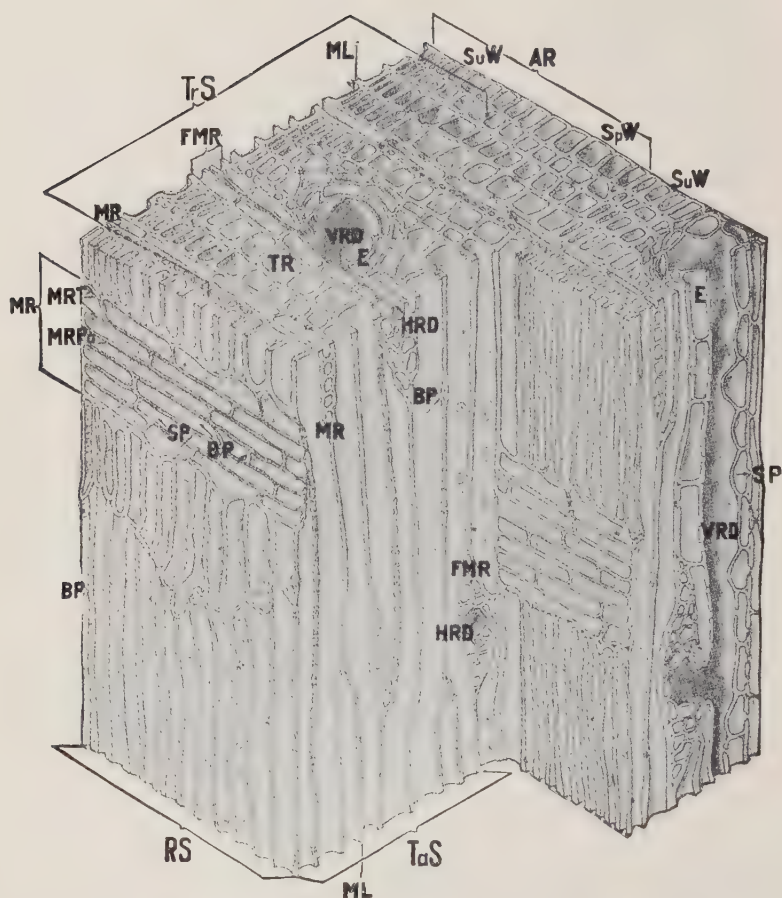


FIG. 39.—Diagram of a typical coniferous wood. *TrS*, transverse section; *RS*, radial section; *TaS*, tangential section; *AR*, annual ring; *SuW*, summer wood; *SpW*, spring wood; *MR*, xylem ray; *TR*, wood tracheids; *E*, secretory cell; *TMR*, fusiform xylem ray; *MRPa*, xylem ray parenchyma; *SP*, simple pits; *BP*, bordered pits; *HRD*, horizontal resin duct; *VRT*, vertical resin duct; *MRT*, xylem ray tracheids; *ML*, primary wall. (After chart by United States Forest Products Laboratory.)

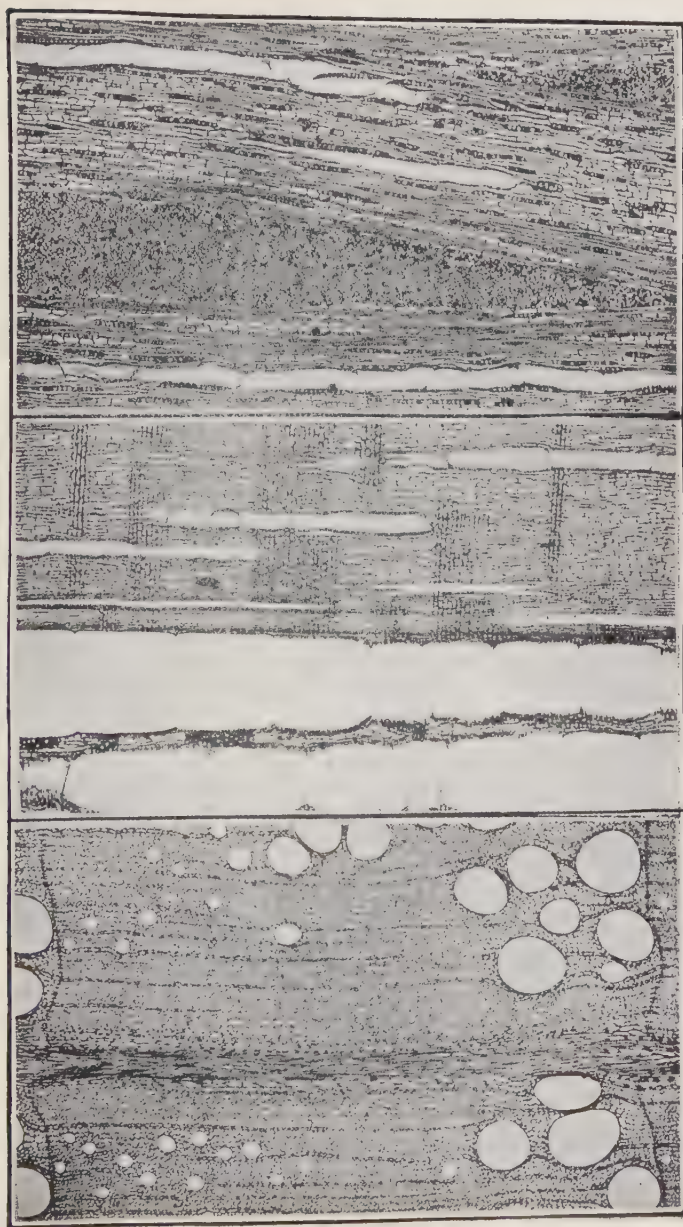


FIG. 40.—Cross (left), radial (middle), and tangential (right), sections of the wood of red oak (*Quercus rubra*). (Photographs by United Forest Products Laboratory, Madison, Wis.)

the formation of xylem and phloem and produce bands of parenchymatous cells which form the vascular rays.

The Cork Cambium or Phellogen.—The **cork cambium** is a lateral meristem similar in some respects to the cambium ring. It usually arises in the cortex just below the epidermis, generally from collenchyma cells which become meristematic and by repeated tangential divisions (Fig. 37) produce daughter cells on both sides. The outer daughter cells are transformed into cork

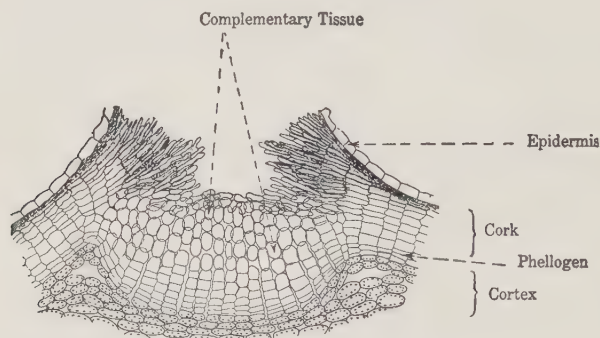


FIG. 41.—Transverse section of lenticel of two-year-old stem of elder. (*Sambucus nigra*.) (After Haberlandt.)

cells. These die soon after suberization. The inner daughter cells which are added to the cortex are cells which remain alive for some time and are otherwise similar to the cortical cells. The phellogen and the interfascicular cambium (page 59) are spoken of as **secondary meristems**, since they originate from cells which have previously existed in the differentiated condition for some time. The primary meristems originate directly from the promeristem.

Lenticels.—Due to the impervious nature of the cork layer formed beneath the epidermis of stems, access of oxygen to cells which underlie the cork would be practically impossible were it not for special ventilating regions in the cork. These regions lie just beneath the stomata. They consist of masses of large thin-walled cells, among which are intercellular spaces, and which by

enlargement finally break through the epidermis and project slightly above the surface of the stem. Such regions are known as lenticels. (See Fig. 41.)

THE HERBACEOUS DICOTYLEDON TYPE OF STEM

In the development of their tissues from the promeristem and the primary meristems, herbaceous dicotyledonous stems are similar to woody dicotyledon-gymnosperm stems. In structure they resemble closely young portions of the woody stems of the dicotyledon-gymnosperm type. The amount of vascular tissue generally is relatively less and the pith and the cortex relatively greater in extent than in woody stems. The type of stem having distinct vascular bundles separated by pith rays and with or without interfascicular cambium, occurs somewhat more frequently among species with herbaceous stems than it does in woody plants. In some cases the vascular tissue is in distinct bundles near the tip of the stem and in a hollow cylinder near the base. (See Fig. 43.) The rigidity of herbaceous stems and of the young parts of woody stems is largely due to the high turgidity of the living cells composing them, rather than to the stiffness of the xylem and other mechanical tissues which are relatively deficient in such stems. High turgor maintains the form of the individual cells and thus gives rigidity to the whole stem but when there is water shortage cell turgor decreases and the cells, becoming distorted under the weight of the stem and of the leaves and other organs which it supports, wilts and droops.

High turgor in living cells tends to stretch them and to enlarge them in all directions. But certain cells, particularly those of the epidermis and the fibers of the cortex and pericycle, can not stretch much on account of their thickened walls, while others, such as those of the pith and parenchyma cells in general, are prevented from stretching or otherwise enlarging by their attachment to or enclosure in less extensible tissues. Thus tissue tensions come to exist in such stems and if the outer less

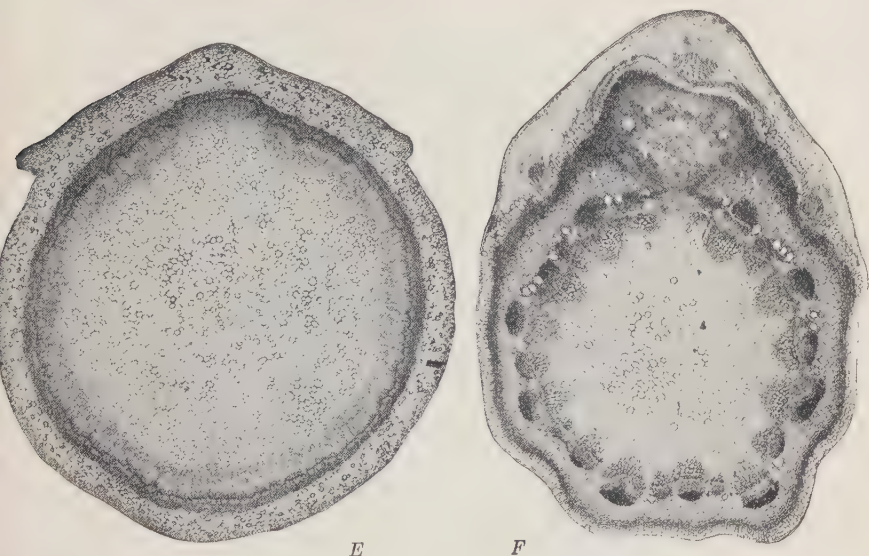
extensible tissues of a herbaceous stem or petiole are freed from the inner tissues it will be found that the release of the tensions



FIG. 42.—Types of dicotyledonous stems. *A*, tree with continuous vascular cylinder, *Liquidambar*. *B*, tree with distinct vascular bundles, *Platanus*. *C*, woody vine with vascular cylinder, *Lonicera*. *D*, a woody vine with distinct vascular bundles, *Clematis*. (After Sinnott and Bailey, from Eames and MacDaniels, *An Introduction to Plant Anatomy*, McGraw-Hill Book Company.)

has been followed by a slight shrinking of the outer tissues and an elongation of the pith. If a ten centimeter piece of turgid

stem is thus treated the outer strips of tissue may be found to be only ninety-eight millimeters long while the pith may be longer by five or six centimeters than it was when the piece was intact. (See Fig. 44.)



E

F

FIG. 43.—Types of dicotyledonous stems (continued). Herbaceous stems. *E*, with continuous vascular cylinder, *Digitalis*, and *F*, with distinct vascular bundles, *Artemisia*. (After Sinnott and Bailey, from Eames and MacDaniels, *Introduction to Plant Anatomy*, McGraw-Hill Book Co.)

THE MONOCOTYLEDON TYPE OF STEM

As in the stem types already discussed, the promeristem of the growing point of monocotyledons, corn for example, differentiates into protoderm, procambium and ground meristem. The protoderm becomes a single epidermal layer which does not differ essentially from that of other seed plants. The procambium always occurs in numerous strands and remains thus, forming many vascular bundles, never a hollow cylinder as it does in most gymnosperm and dicotyledon stems. The procambium strands are not even arranged in a ring, but are scattered through-

out the ground meristem. All the procambium cells differentiate into xylem and phloem elements and none remain in the meristematic condition as do those of the vascular cambium of gym-



FIG. 44.—Flower stalks of Calla lily (*Richardia*) in each of which a central cylinder of tissue has been freed from the tissue around it but left intact at the base, in order to demonstrate the tissue tensions which exist in many plant organs. In the case of each of the two flower stalks, after trimming the end off square with a razor the cylinder of tissue was freed from the outer tissue to a depth 10 centimeters by means of a sharp, thoroughly wetted cork borer. In the case of the stalk to the right the outer tissue was then cut into lengthwise strips which were left attached at the base.

nosperms and dicotyledons. Bundles of this sort, which are without a cambium, are called closed bundles (Fig. 46). Those of other seed-bearing plants in which a cambium lies between the xylem and the phloem are called open bundles.

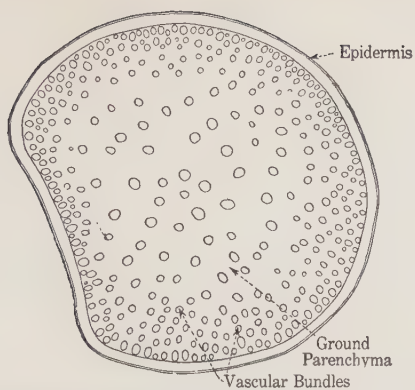


FIG. 45.—Diagrammatic cross section of the stem of corn (*Zea mays*)—an herbaceous monocotyledonous plant.

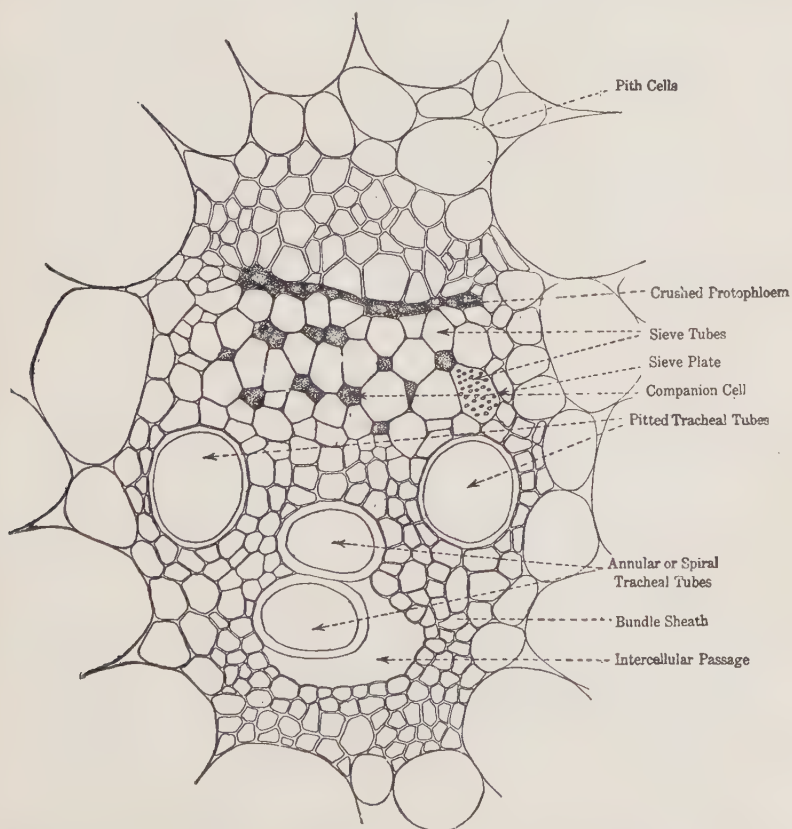


FIG. 46.—Cross section of a vascular bundle of the stem of corn (*Zea mays*) — a monocotyledon.

There is no distinct demarcation between cortex and pericycle in most monocotyledonous stems. Moreover, since the numerous vascular bundles are scattered throughout the stele, these stems lack a definite pith.

Due to the absence of a cambium, monocotyledonous stems in general are not able to add to the quantity of xylem and phloem nor to increase to any considerable extent the number of cells in any of the other tissues. Therefore such stems do not increase much in thickness as they increase in age. What growth in thickness they do have is due almost entirely to enlargement of cells differentiated from the primary meristems. Whereas in the stems of perennial dicotyledons and gymnosperms conducting elements of the xylem and phloem may cease to function within a few years, and are replaced by younger conducting elements, in perennial monocotyledons these elements retain their ability to transport materials throughout the life of the plant.

The stems of grasses are called **culms** (Fig. 75). They are usually cylindrical in shape, and when mature their internodes are generally hollow, although sometimes, as in corn, they are solid.

FUNCTIONS OF STEMS

The primary functions of the stem are **support** of the leaves and **conduction** of water and raw materials for food manufacture to the leaves, and of food from the leaves. Secondary functions, that is those functions which the stem may carry on but which are at least equally characteristic of other organs, are **food storage** and **food manufacture**.

Support.—The stem supports the leaves and so distributes them through space that they are in positions favorable for light absorption and thus conducive to photosynthesis. The elevation of the flowers on the stem favors both the transfer of pollen by wind and insects and the dissemination of seeds.

Conduction.—The stem conducts (a) water absorbed by the root from the soil, (b) dissolved inorganic substances also taken

up from the soil by roots, and (c) various foods manufactured in the plant. In angiosperms the tracheal tubes are the chief carriers

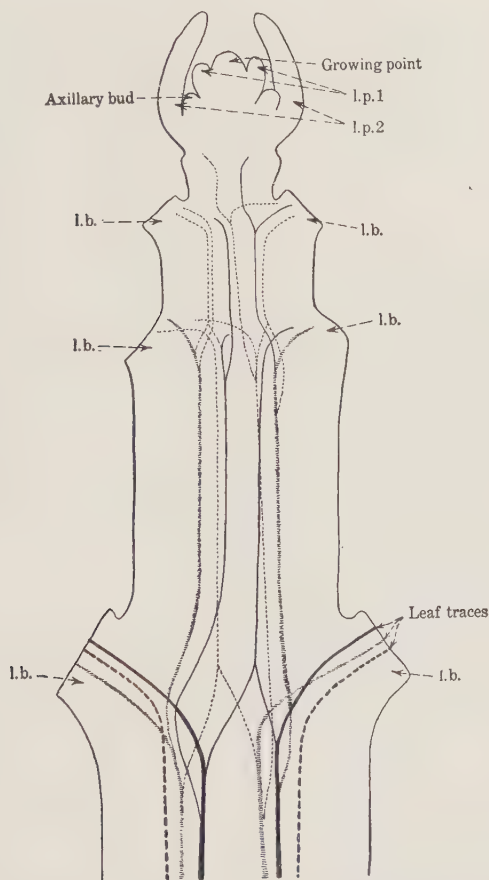


FIG. 47.—*Clematis* species. Diagram of several nodes and internodes and the terminal bud showing the vascular bundles of the stem and their branches (leaf traces) passing out into the petioles. *l.b.*, leaf bases; *l.p.*, rudimentary leaves. (After Nägeli.)

of water and inorganic salts from the roots to the leaves. This function is shared to some extent, however, with the tracheids,

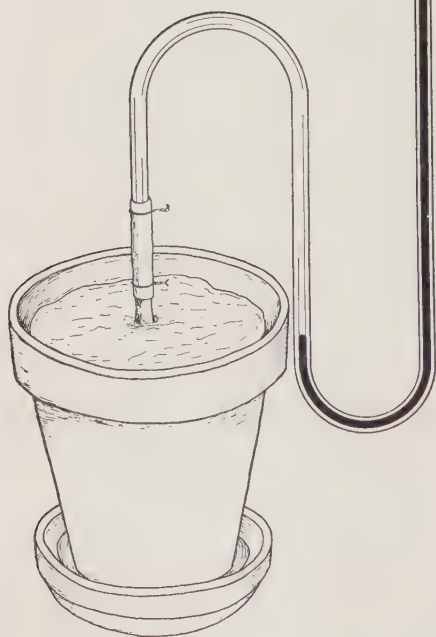


FIG. 48.—Demonstration of root pressure. The difference in the elevation of the mercury in the arms of the U-tube is a measure of the root pressure in the decapitated plant. The liquid in the tube in the part nearest the stem is water or sap.



FIG. 49.—Method of demonstrating the lifting power of transpiring leaves. The elevation of the mercury column in the glass tube above that in the dish is a measure of this power

and in the gymnosperms, which lack tracheal tubes, tracheids are the only elements for conduction of water and inorganic salts longitudinally.

The rate of movement and path of water and inorganic salts up the stem may be roughly ascertained by placing a leafy branch, which has been cut under water, in a solution of eosin, indigo carmine, or any one of various other dyes. After a short time a series of cross sections at different elevations or a longi-

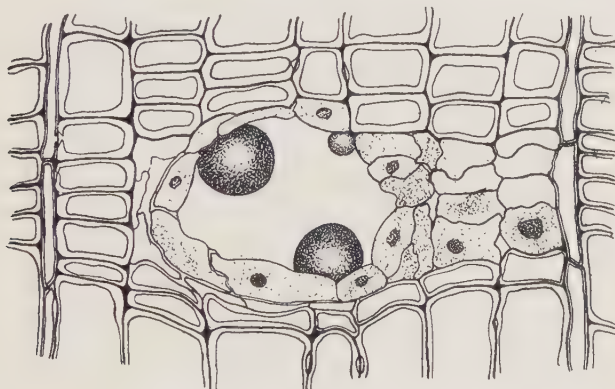


FIG. 50.—Portion of a cross section of wood of *Pinus strobus* showing a resin duct containing globules of resin.

tudinal section of the stem will show that the solution is present only in tracheal tubes and tracheids, and in the time allowed has risen to a certain height.

Destroying the pith and the parts outside the woody cylinder does not interfere with the upward conduction of water and solutes. Lateral transfer of these from the wood to the other tissues of the stem is probably by means of wood parenchyma cells, vascular rays, and pith rays when present.

The Factors Responsible for the Rise of Sap in Stems.—The quantity of water which may be transpired from a tree in a single growing season and which must therefore be conducted up the stem during that time is astonishingly great. This water

is often raised to great heights, as in *Sequoia sempervirens*, and the question of how it is done is one to which there is still no satisfactory answer.

According to one theory the sap rises by reason of a pressure (root pressure) set up in the conducting tissue by the water absorbed into the root. Such pressure is, however, insufficient

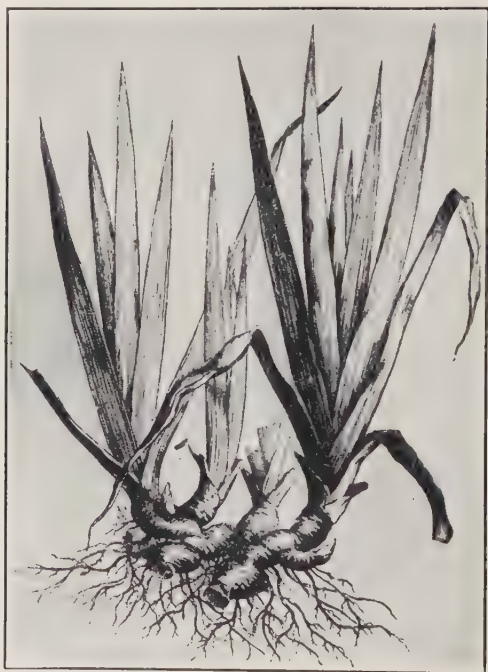


FIG. 51.—Iris plants, showing the rhizomes with leafy shoots and roots. (From Bocquillon.)

to explain the rise of sap to the tops of tall trees. Moreover, experiments show that the sap is pulled up from above, not pushed up from below.

Capillarity, the property of most liquids to rise in fine tubes, has been suggested as an explanation of the rise of water in the tracheal tubes and tracheids of the stem. These tubes are of too

large bore to raise water to any great height and, even if they were fine enough, the viscosity of the water columns would be too great to permit of their movement except under immense pressure.

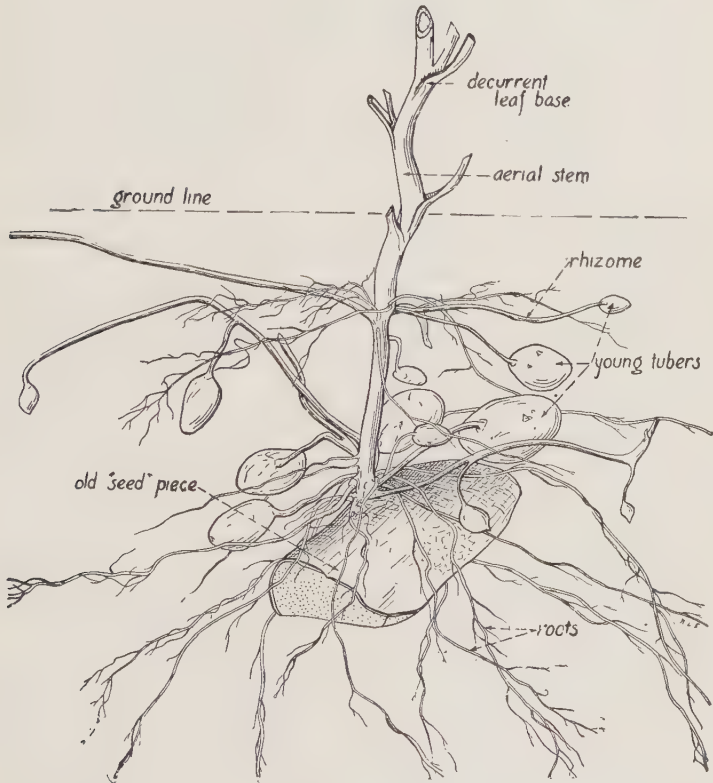


FIG. 52.—Portion of "seed piece" of a potato tuber and of a potato plant which has grown from it. (After Robbins, *Botany of Crop Plants*.)

Another theory invalidated by experiments is that of the so-called **pumping action of the living cells of the wood**.

The most satisfactory theory thus far advanced is that of transpiration pull and water cohesion. The principal factors of this

theory are as follows: (1) Loss of water from the cells of the leaf by transpiration tends to maintain a high concentration of solutes in these cells, that is, a high osmotic pressure. (2) This results in the leaf cells withdrawing water from the dilute solutions (sap) in the tracheal tubes and tracheids. (3) Accordingly, a pull is exerted on the upper end of the water column in the conducting

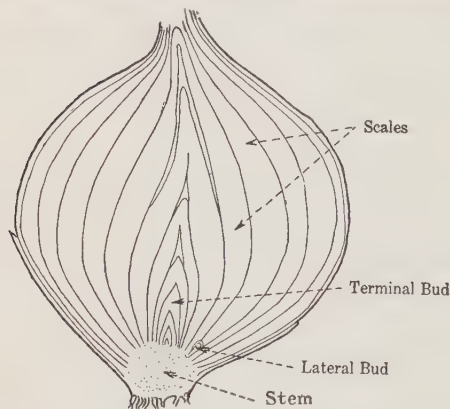


FIG. 53.—Median longitudinal section of an onion bulb.

elements and the entire sap stream is raised. This explanation requires that there be a continuous water column from root to leaf and that this water column have sufficient tensile strength to hold itself intact, that is to say, to prevent its breaking under the strong pull necessary to raise the long column. Experimentation seems to show that

these requirements are met by the condition existing in the stem.

Conduction of Food.—As already stated, there is evidence that conduction of foods, including soluble carbohydrates, proteins, and amino acids from which proteins are synthesized, takes place chiefly in the phloem. The removal of a band of bark down to the xylem finally results in the death of the plant through starvation of the roots. If only outer portions of the bark are removed and the phloem is left intact, the roots do not suffer and there appears to be no marked interference with food conduction. Furthermore, chemical tests show that various foods are present in larger quantities in the sieve tubes than would be likely if they did not serve for food storage or transfer. Although the sieve tubes are undoubtedly the principal food-conducting elements of the phloem, phloem parenchyma may also convey

carbohydrates and amino acids longitudinally. Foods pass transversely in the stem along the vascular rays.

Storage in Stems.—Various substances, such as water, food, and waste products, may accumulate in stems. These stored products may or may not be utilized later by the plant. The fleshy stems of such plants as cacti or begonia accumulate large quantities of water in the cells of the cortex or pith.

Stems may also serve as storage places for food. Subterranean stems, such as tubers, rhizomes, and corms are especially adapted for this. Starch is the most common form of food stored in stems, but cane sugar (sucrose), reserve fats, and proteins are also present. The starch is formed within the leucoplasts of the storage cells when surplus sugar (probably glucose) reaches these cells from the leaves. Before the reserve carbohydrate can leave the storage organs to be used elsewhere in the plant it must be digested to form sugars again.

Propagation by Means of Stems.

—Many plants may be propagated (multiplied) by means of stem pieces and even under natural conditions pieces of stems often become detached and developed into new plants. Propagation by means of cuttings, whether of stems or of other vegetative structures, is of great importance in agriculture, because by this method new plants which are true to type, may readily be secured.

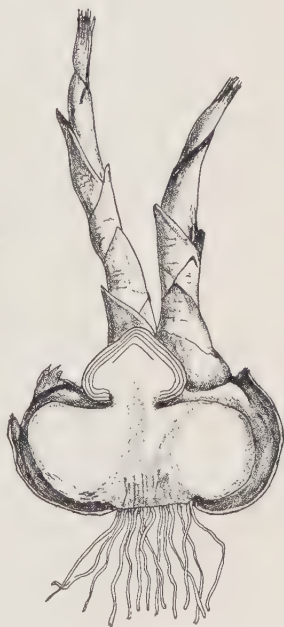


FIG. 54.—Corm of crocus, in longitudinal section. (Redrawn from Figurier.)

STEM MODIFICATIONS

Ordinarily we think of a stem as a cylindrical organ growing more or less erect. However, there are many modifications of stems differing so much in form and in other respects from the ordinary type that they are scarcely recognizable as stems, and careful study of their origin and structure is often necessary to identify them as such. Examples of these modified stems are rhizomes, tubers, bulbs, corms, runners and tendrils. Rhizomes

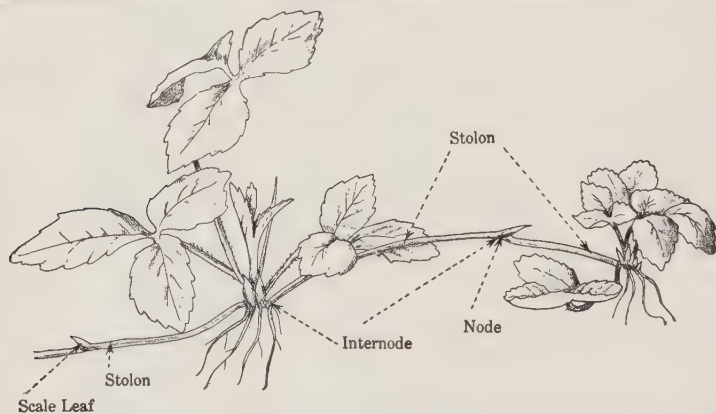


FIG. 55.—A strawberry (*Fragaria*) plant showing propagation by means of stolons. Somewhat diagrammatic.

(or rootstocks) are elongated, horizontal underground stems, such as those of *Iris* and most ferns, and are generally rich in stored food. Tubers are much enlarged, short, fleshy underground stems, usually lacking roots and produced at the ends of rhizomes. The most familiar example is the Irish potato (*Solanum tuberosum*). A bulb consists of a short, flattened, or disk-shaped underground stem, from which arise numerous fleshy scale-like leaves filled with stored food. The common onion (*Allium cepa*) is a typical example. A corm is a short, solid, vertical, enlarged underground stem, usually flattened from top to bottom. It bears a cluster of thick fibrous roots on the lower side, and a tuft

of leaves on the upper. Illustrative plants are gladiolus and crocus. A runner (or stolon) is an elongated stem which grows horizontally along the surface of the ground. The strawberry (*Fragaria*) naturally propagates itself by means of such runners.

Occasionally stems are modified into tendrils as in the Fox grape, spines as in the honey locust, or leaf-like photosynthetic organs as in the cactus.

CHAPTER IV

THE ROOT

DUE to strong superficial resemblances root and stem are distinguished only with difficulty in some Spermatophyta. In general, however, the following criteria can be applied.

ROOTS

Roots rarely grow upward.

Roots are not divided into regions (like nodes of stems) from which branches may arise, alternating with regions from which branches do not arise.

The branches of roots originate within the root from which they arise.

The growing point of the root is covered by a special protective structure, the root cap.

STEMS

Stems rarely grow downward.

Stems are made up of alternating nodes (from which leaves and branches may arise) and internodes, which are leafless and without branches.

Branch stems originate at the surface of the stems from which they arise.

The growing point of the stem is not protected by any special structure but by rudimentary foliage leaves and frequently by bud scales (modified leaves) also.

In addition to these points of contrast, roots and stems differ greatly in the arrangement of their primary tissues. However, those roots which by the development of cambium undergo secondary growth in thickness come to resemble old woody stems in their anatomy.

Kinds of Roots.—According to their origin, roots may be classified as **primary**, **secondary**, and **adventitious**.

The primary root of a plant is the one which develops from the radicle (rudimentary root) of the embryo. It is the first root and in many species remains the principal one throughout the

life of the plant. Branches of it are called secondary roots. All roots which do not arise directly from the radicle or as branches of the primary root are spoken of as adventitious.

Classification of Root Systems.—In many plants, especially among the monocotyledons, the primary root does not become the principal root but stops growing while the plant is still young. In such cases the functions of anchorage and absorption are taken over by numerous adventitious roots which grow out at the base of the stem. There results what is spoken of as a *fibrous root system*. This is characteristic of the grasses, palms and many other kinds of plants.

When the root system consists principally of an actively growing primary root with its branches (secondary roots) it is spoken of as a **tap root system** or **primary root system**. The outstanding examples of this category are found in the carrot (*Daucus*), beet (*Beta*), radish

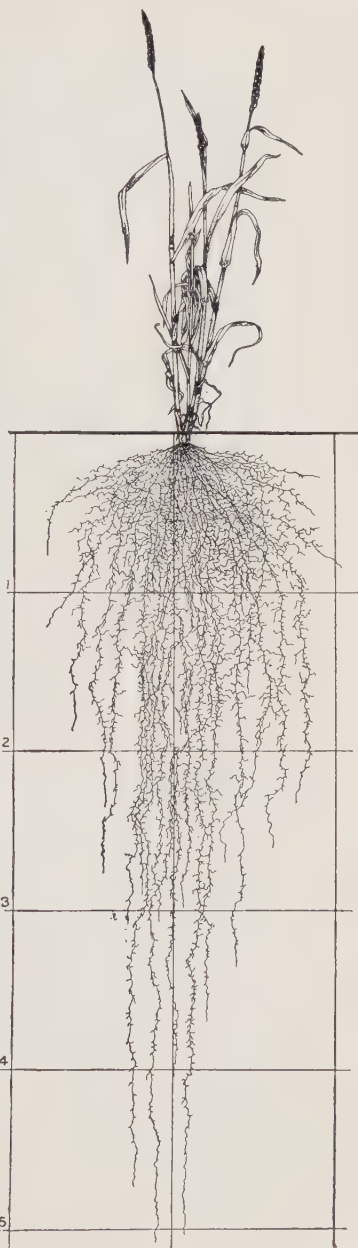


FIG. 56.—Fibrous root system of wheat. The numbers indicate depth in feet. (After Weaver, Carnegie Institution of Washington, Pub. No. 316.)

(*Raphanus*), turnip (*Brassica*), and other such plants in which the primary root is greatly enlarged for food storage. Nevertheless, the prevailing condition is that of dandelion (*Taraxacum*) and oak (*Quercus*), in which the primary or tap root is not so conspicuously enlarged.

The Form of the Root System.—

Just as we recognize great differences in the form of the shoot systems of our common plants, so we find conspicuous differences in the form of root systems. (Figures 56 and 57 illustrate various types of root systems.) Those of cereals and most grasses are shallow and in general assume a broad, pyramidal form, with the apex of the pyramid at the ground line. The sugar beet (*Beta vulgaris*), on the other hand, has a deep root system, the general form of which is rectangular.

Though shallow root systems are characteristic of certain species of plants and deep root systems of others, the depth of the root system in many cases varies greatly with soil conditions. Plants living in a dry region, where they must depend largely on occasional showers for water, profit by a shallow root system with great numbers of roots in the first few inches of soil, for

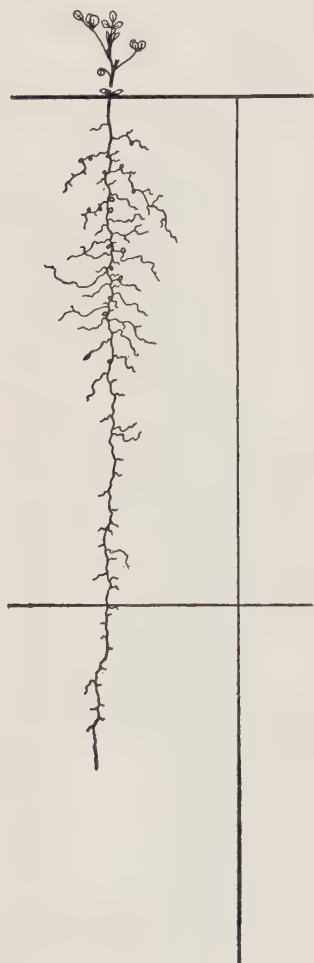


FIG. 57.—Tap root system of young sweet clover plant (*Melilotus*). The distance between the horizontal lines represents one foot. (After Weaver, Carnegie Institution of Washington, Pub. No. 316.)

beyond this the water seldom penetrates. On the other hand, for plants growing in regions where they must depend principally on water deeper in the soil the deep root system is more advantageous. As far as firm anchorage of the plant is concerned the deep root system is obviously more efficient than the shallow.

STRUCTURE OF ROOTS

External Features.—The root is an almost cylindrical structure, tapering very gradually from its base, where it is attached to the stem or a larger root, toward its free end or **root tip**. It is in the four to six centimeters of the free end that growth in length, water absorption, and most of the primary development of the tissues take place. This part of the root may for convenience in describing it be divided (see Fig. 58) into the following regions, beginning at the very tip:

- The root cap,
- The growing point,
- The region of elongation,
- The region of root hairs.

The **root cap** consists of a thimble-shaped mass of cells covering the end of the growing point. As a protective structure it corresponds to the rudimentary leaves and bud scales of the stem. But whereas the latter prevent injury due in a large degree to water loss, the root cap is concerned chiefly with mechanical injury. As the root tip is constantly forced through the soil, which consists largely of pieces of rock, the root cap bears the brunt of the abrasion. To compensate for this wearing away cells are constantly being added to it by the growing point.

The **growing point**, as in the stem, consists of tissue (promeristem) in which active cell division continues as long as the root grows. In most cases this region of the root is about a millimeter long. Growth in length takes place in this region but at a very much slower rate than in the region of elongation just behind it.

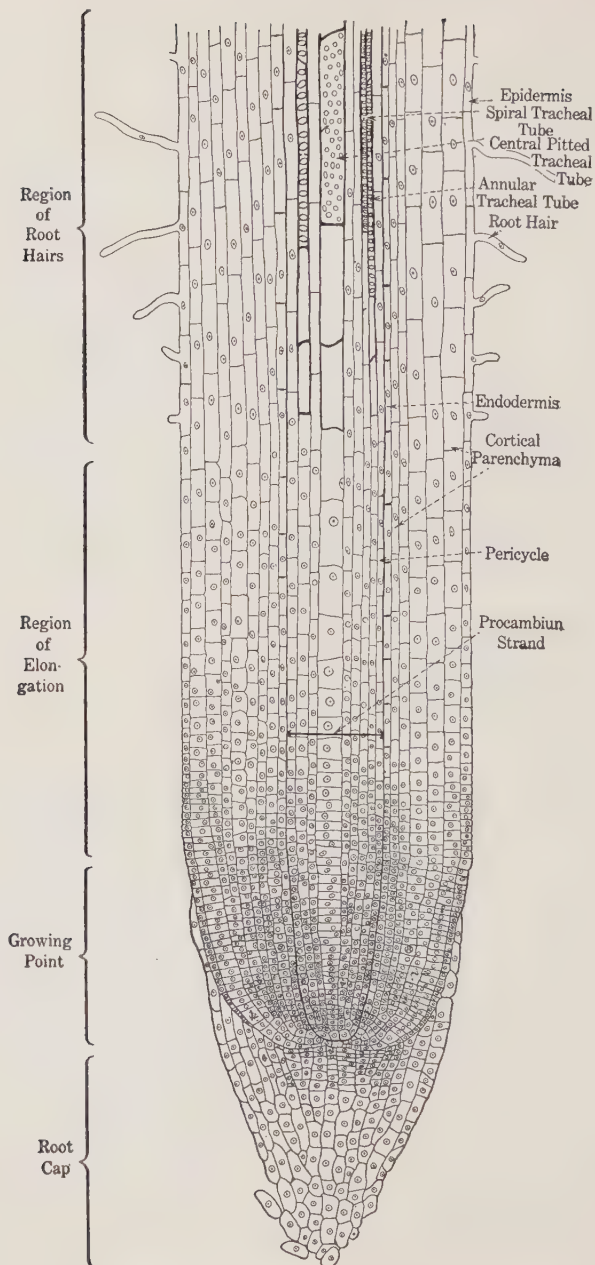


FIG. 58.—Longitudinal section of the root of barley (*Hordeum sativum*).

As the result of active cell division, the number of cells in the growing point tends to increase. We have seen that some of these cells are added to the root cap. Others are constantly passing over into the region of elongation.

In the **region of elongation** the cells produced in the growing point undergo very rapid growth in length as the result of the

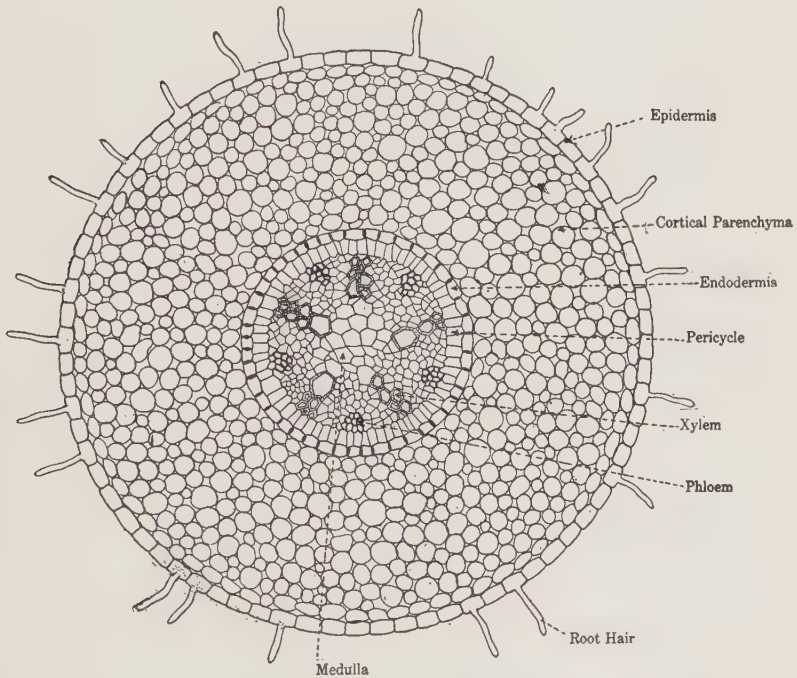


FIG. 59.—Cross section (diagrammatic) through the root-hair zone of a young dicotyledonous root.

absorption of large quantities of water and the stretching due to the high turgor thus developed. This region of the root is generally from two to five millimeters long.

In the **region of root hairs** elongation has ceased and the surface of the root becomes clothed with a dense outgrowth of

hairs. These structures are not only of great importance in connection with the absorptive function of the root but also with anchorage. It is in this zone that the cells inside the root, which were produced in the growing point and which increased greatly in length in the region of elongation, differentiate into tracheal tubes, tracheids, sieve tubes, and the various other permanent tissues of the root. On this account it might be spoken of as the region of maturation.

The four regions which have been briefly described are spoken of collectively as the **root tip**. In the part of the root behind the tip the root hairs are withered and dead, for the life of each root hair is but a few days, and the older ones die off as new ones are produced at the lower end of the root-hair zone. In the mature part of the root growth in length never takes place; instead there sometimes is an actual shortening. It is in this region that secondary roots make their appearance.

Anatomy of the Root.—Since roots are much more uniform in their internal structure than are stems we shall not have to study several types, but merely consider a series of cross sections from the growing point to the mature region.

The Growing Point.—This is composed of typical meristematic cells, thin walled, all very much alike, practically without intercellular spaces. During that time of the day when cell division is most active a great many nuclei are in some stage of mitosis.

The Region of Elongation.—Though most of the cells in this region are still meristematic they no longer are uniform, for some differentiation has taken place. The single layer of surface cells constitutes the **protoderm**. The cylindrical group of cells in the center of the section is now the procambium, and between this and the protoderm is the ground meristem. It will be recalled from the discussion of the anatomy of the stem that these three meristematic regions are spoken of as the primary meristems.

The Region of Root Hairs.—In this region the following primary permanent tissues are present:

1. The **epidermis** (derived from the protoderm) with its root hairs.
2. The **cortex** (derived from the ground meristem), the innermost layer of which is the endodermis.
3. The **stele**, consisting of:

The **pericycle**, which is derived from the ground meristem, and the **xylem** and **phloem** derived from the procambium.

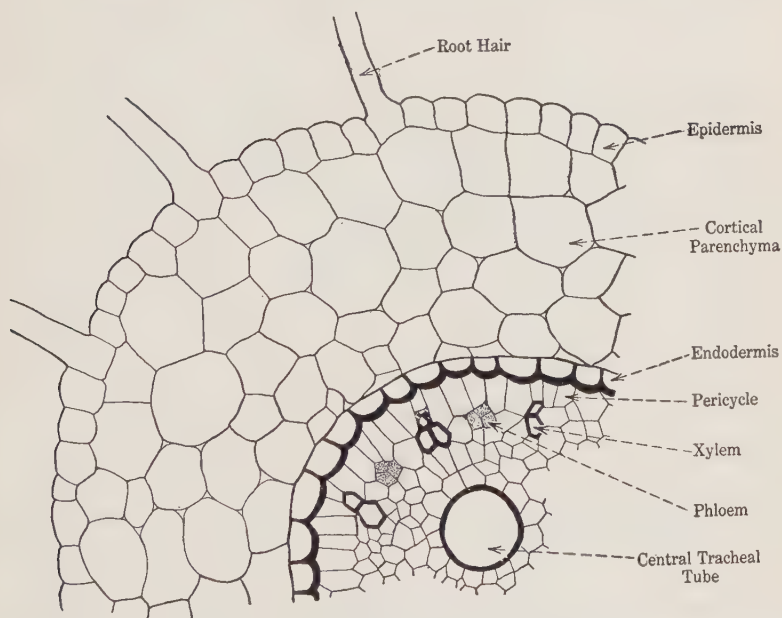


FIG. 60.—Part of a cross section of the root of barley (*Hordeum sativum*), through the root-hair zone. (Redrawn from Percival.)

The epidermis consists of a single layer of cells from which the root hairs arise. The cortex is composed of numerous layers of parenchyma cells and of a single innermost layer, the endodermis. The cells of the latter frequently have their inner and radial walls thickened and impregnated with cutin and suberin.

The arrangement of the vascular tissues is of the radial type

(Fig. 59). The xylem elements are in groups which radiate from the center of the root. Alternate with, and in the angles formed by these radiating xylem groups are groups of phloem elements.

Growth in Diameter of Root.—In most monocotyledons and in many annual dicotyledons there is no secondary increase in thickness in the roots. In such plants sections through older parts of the root would be essentially like a section through the region immediately above the root-hair zone. Here the root

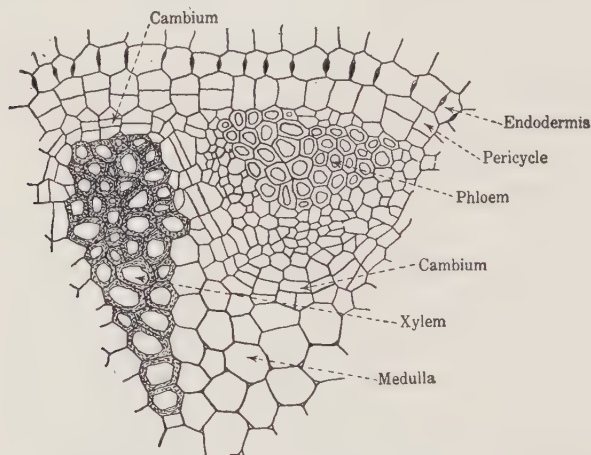


FIG. 61.—Cross section of a portion of the central cylinder of a primary root of horse-bean (*Vicia faba*), showing the origin of the cambium. (Redrawn from Haberlandt.)

hairs are withered and dead, while the epidermal cells and frequently several adjacent layers of cortex cells are becoming suberized and function as a protective layer. In perennial dicotyledon and gymnosperm roots a cambium arises and secondary increase in thickness normally occurs. Certain of the cells adjacent to the outside of the xylem and phloem strands, including those of the pericycle lying just outside of the xylem masses, become meristematic and form a cambium ring. As a result of the activity of this cambium ring, vascular bundles

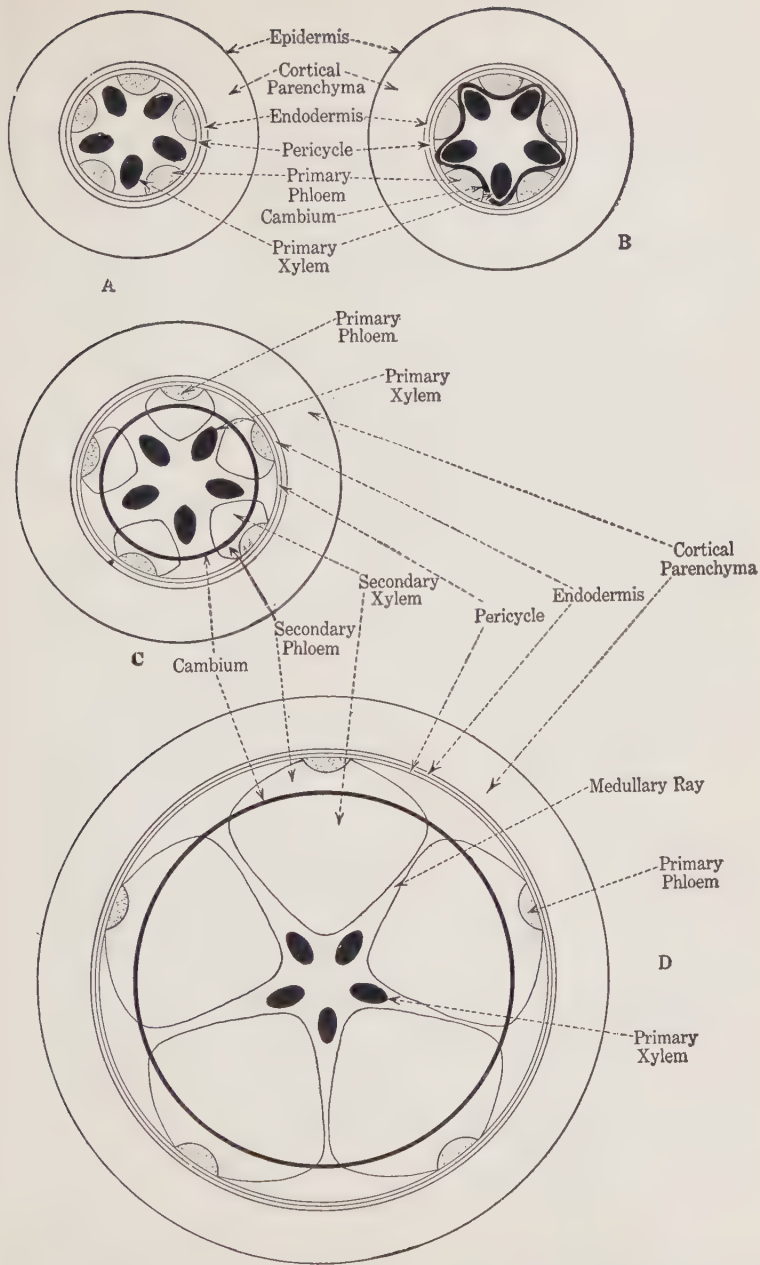


FIG. 62.—Diagrams showing stages in the secondary increase in thickness of a root. *A*, before the appearance of cambium. *B*, the formation of the cambium ring. *C* and *D*, stages in the development and growth of secondary phloem and xylem. Secondary increase in thickness due to the activity of phellogen is not shown.

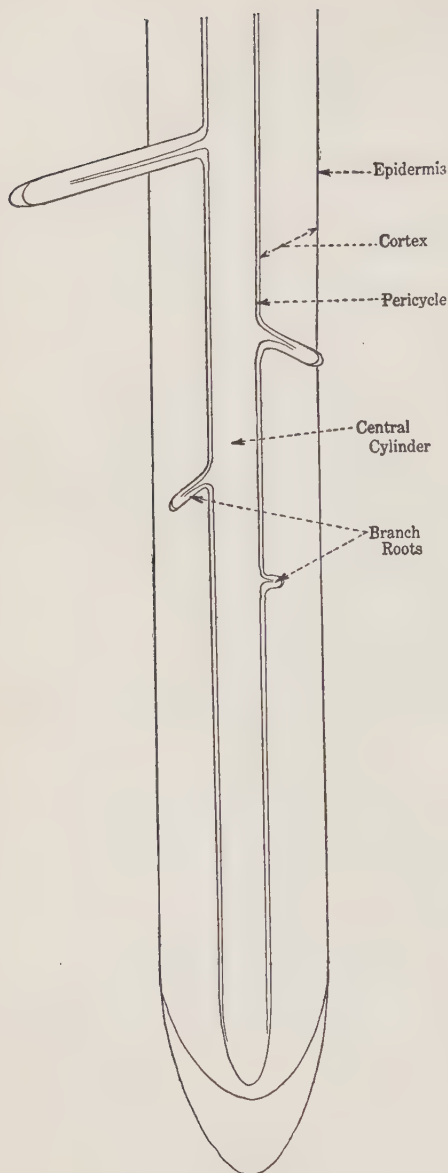


FIG. 63.—Diagram showing the origin of branch roots and their emergence from the main root.

similar to those of dicotyledonous and gymnosperm stems are produced. (See Fig. 62.)

Soon after the vascular cambium makes its appearance, certain cells of the pericycle undergo repeated division and form a **phellogen** or **cork cambium**. The cork cambium produces cork externally and secondary cortex internally. All the tissues which originally lay outside of the pericycle die soon after cork formation commences. As a result of the activities of these two cambiums, the old root comes to resemble closely an old stem in its structure.

Root Branching.—It will be recalled that the outermost tissue of the stele is the pericycle. It is in this layer that branch roots have their origin. The first evidence of the formation of a branch root is the tangential division of

certain pericycle cells (Figs. 64, 65). These form a group of meristematic cells, which in turn develop a root tip with root cap. The root tip makes its way outward through the cortex and the epidermis, and reaches the surface. (See Fig. 63.) Such branch roots do not emerge into the soil until elongation has ceased in that part of the main root from which they arise.

Root Hairs.—A root hair is a lateral protuberance of an epidermal cell (Fig. 66) having the form of a slender tube closed at the free end. A root hair and the epidermal cell from which it grows are not separated by a wall and together constitute a single branched cell with a single protoplast. Though tending toward cylindrical form root hairs may become greatly contorted in their growth between and around soil particles. Root hairs vary in length from a fraction of a millimeter to seven or eight millimeters, and have delicate walls of pure cellulose. These are lined by only a thin layer of cytoplasm so the vacuole or vacuoles are relatively large. All the materials that enter the

plant from the soil must pass through the walls and the cytoplasmic membranes of the root hairs or epidermal cells. From the root hair, the absorbed materials are passed on to cells of the root cortex, to the pericycle, and then into the conducting elements of the xylem. By these they are carried to various parts of the plant.

Functioning root hairs are not found along the full length of

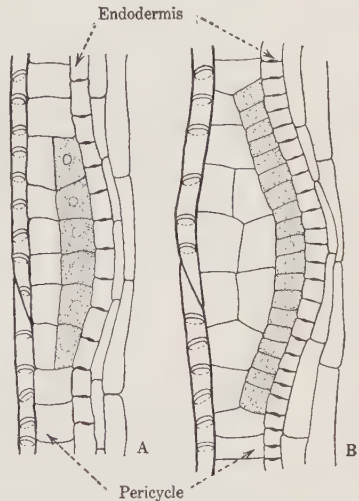


FIG. 64.—Two stages in the initiation of a branch root. Certain pericyclic cells (here stippled) become meristematic and undergo tangential division. They thus initiate the growing point of a new branch root. (Redrawn from Van Tieghem.)

the root, but appear as a white, fuzzy coating on a definite zone, known as the **root hair zone** (Fig. 67). If we proceed backward

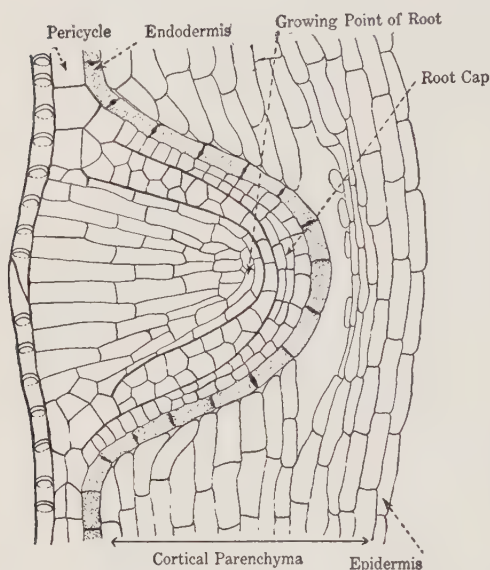


FIG. 65.—Stage of branch-root development later than those shown in Fig. 64. Note that in this figure it is the cells of the endodermis which are stippled, not certain pericyclic cells as in Fig. 64. (Redrawn from Van Tieghem.)

are constantly brought into contact with new soil particles as new soil regions are invaded. This is of advantage to the plant, first because new stores of water and salts thus become available to the root hairs, and second, because these new soil regions are devoid of any deleterious substances which may accumulate in the neighborhood of the old hairs.

FUNCTIONS OF ROOTS

The functions of the root system are absorption, conduction, anchorage, and storage. These four processes will be described in the order named.

from the growing point we will find this zone lies immediately beyond the region of elongation. Root cap, growing point, and region of elongation all are devoid of root hairs. Root hairs are short-lived, functioning for only a few days or weeks. New hairs are constantly formed at the lower end of the root-hair zone, while the old hairs at the upper end are dying. The root-hair zone advances through the soil as the root grows. In this way root hairs

In considering the process of absorption we shall discuss:

- (a) Absorption of water;
- (b) Absorption of inorganic salts.

Absorption of Water.—Water performs many essential rôles in the plant, chief of which are the following:

1. It is a necessary component of protoplasm, constituting about 80 to 90 per cent of the weight of active protoplasm.

2. It is an essential raw material for food manufacture (see page 117).

3. It serves as a solvent of gases (oxygen and carbon dioxide).

4. It serves as a medium of transportation of raw materials and foods from place to place in the plant, since their transport can take place for the most part only in solution.

5. It makes possible the maintenance of turgor in living cells, and the plant functions normally only when the cells are distended with water.

Water enters the plant through the root hairs, this entry being known as **water absorption**. Water passes out of the plant principally through small openings (stomata) in the surface of the leaves, and we speak of this water exit as **transpiration**. From roots to leaves there is a continuous stream of water through the plant. Its rate of flow may be restricted at two points, the point of entry and the point of exit. Too much transpiration and too little absorption are the principal dangers to which the plant is exposed.

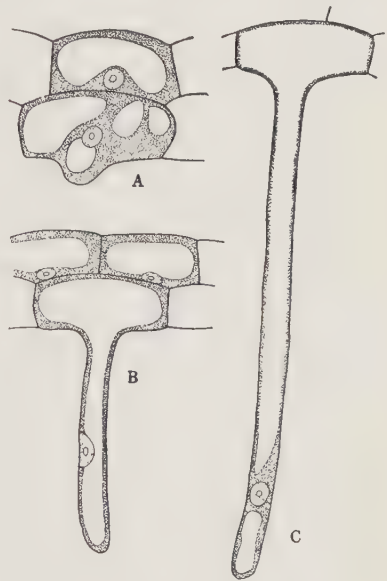


FIG. 66.—Stages in the development of a root hair. (After Frank.)

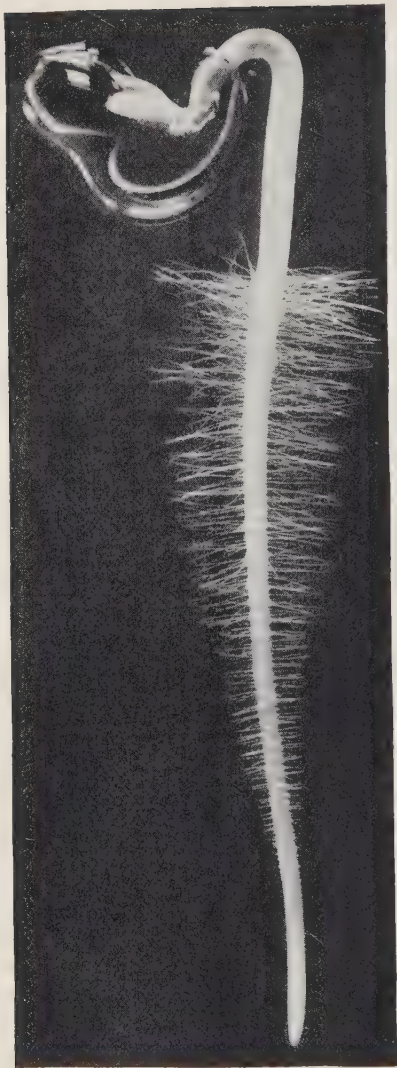


FIG. 67.—Seedling of garden cress (*Lepidium*) grown in moist air. Root hairs in various stages of development can be distinguished behind the region of elongation. Surrounding the cotyledons is the swollen gelatinous mass derived from the seed coats. Magnification 6 $\times$.

All substances, either gases or solids, which enter the plant from the soil must be in solution in water, and must pass through the wall of the root hair and also through the cytoplasmic membrane which lines the wall. The cell wall, of cellulose, is a permeable membrane. Water and all solutes present in the soil solution can pass through this wall unhindered. The cytoplasmic membrane, however, is semipermeable. Normally the total concentration of the solutes in the cell sap of the root hair is greater than in the soil solution outside the root hair. Under this condition the movement of water is from the soil into the root hair, and this movement of water tends to go on just as long as the concentration within the root hair exceeds that outside. Since the rate of movement of water inward depends upon the relative concentration of the two solutions, this rate tends to decrease as the concentrations of the two solutions become more nearly equal. Water, however, is constantly being withdrawn from root hair

cells to the outermost cells of the cortex by osmosis. This causes the concentration of the cell sap of the root hairs to remain fairly constant.

Factors Affecting the Intake of Water from the Soil.—The principal factors influencing the absorption of water by the plant are the following:

1. *Available Water in the Soil.*—Not all of the water in the soil is available for absorption. In fact, there is no direct relation between the percentage of water in the soil and the amount available to the plant, because this amount varies with the nature of the soil.

2. *Rate of Water Movement in the Soil.*—If the rate of water absorption by the roots is high, and moisture is absorbed by the root hairs from the adjacent soil at a faster rate than soil conditions will allow it to be replaced from more remote soil layers, the soil immediately surrounding the root hairs will attain a water content which will result in wilting and consequently cessation of growth.

3. *Temperature of Soil Water.*—The rate of absorption by the roots of plants is lowered by a decrease in soil temperature. This explains why a plant may wilt in a soil saturated with water when the temperature of the soil falls below a certain point.

4. *Concentration of the Soil Solution.*—Water intake and transport tend to go on as long as the total concentration of the cell sap of the root-hair cells is greater than the total concentration of the soil solution surrounding the root hairs. The greater the differences in concentration between the cell sap and the soil solution, the more rapid the water intake. If the concentration of the soil solution approaches that of the cell sap, the rate of absorption decreases.

5. *Composition of the Soil Solution.*—The influence of the composition of the soil solution upon the rate of intake of water by roots is well shown by many bog plants. In such plants absorption is low in proportion to transpiration. This is held to be due to the presence in bog water of substances somewhat toxic (poisonous) to plants.

6. *Extent of Root System.*—Some plants, alfalfa, for example, do not suffer from drought because of the ability to send their roots into the deeper and moister soil layers. If, on the other hand, the soil extends but a short distance and rainfall is light, plants with shallow root systems are likely to be relatively more successful than deep-rooted species, because they can take advantage of the water that comes to the soil in occasional light showers.

7. *The Rate of Transpiration.*—The amount of water transpired by a plant during a given period is practically equal to that absorbed during the same period. The rate of entrance of water through the roots and its rate of movement in the plant depend largely on the rate of transpiration. Such external conditions as light, relative humidity, temperature, and air movements, which directly influence the rate of transpiration, indirectly affect the rate of absorption.

Absorption of Inorganic Salts.—Land plants derive their inorganic salts from the soil. Among the inorganic salts which occur there, the chief ones used by green plants are nitrates, phosphates and sulphates. Green plants derive nitrogen principally from nitrates; phosphorus from phosphates; and sulphur from sulphates; the other essential elements derived from the soil, potassium, calcium, magnesium, and iron, are taken chiefly from salts occurring in combinations with either nitrogen, phosphorus, or sulphur. These salts can enter the plant from the soil only when they are in solution.

It is important to keep in mind, however, that under similar conditions the **different mineral salts move into the plant independent of the passage of each other and of water.**

Hence we may picture the process of absorption by root hairs as one in which the molecules of water and the dissolved particles of many different salts are independently diffusing through cytoplasmic membranes of the root hair at varying rates, the rates depending in large part upon the quantity of each substance used by the plant.

Whereas substances pass from the soil through a cytoplasmic

membrane into the root hair, it should be pointed out that, with the exception of water and carbon dioxide, substances in the root hairs are unable to pass into the soil.

Conduction by Roots.—Water which is absorbed by the root hairs passes by diffusion into adjoining cortex cells; by the same process it passes across the root from one cortex cell to another to the tracheal tubes and tracheids of the xylem. It is carried upward in these elements to the stem. In the young root xylem and phloem elements occur in radiating groups, the groups of xylem elements alternating with the phloem groups. Hence it is possible for the water to reach the xylem elements from the cortex without first passing across the phloem elements. There is some difference of opinion concerning the path of movement of dissolved mineral salts which are absorbed by the root hairs. The most widespread belief is that they travel in the transpiration stream, but there is some evidence that these solutes



FIG. 68.—Clustered fleshy roots of dahlia.
(From Bocquillon's "La Vie de la Plante.")

are conducted in the phloem. It may be that both xylem and phloem are concerned in the upward movement of mineral salts.

Anchorage.—The roots of a plant are very effective anchorage organs. In most plants all roots perform the triple rôle of absorption, conduction, and anchorage. However there are some plants (cacti, e. g.,) which are equipped with two kinds of roots, those mainly for anchorage and those chiefly concerned with absorption.

The hold which roots have on the soil is well shown in plants of sand dunes; here, where the soil tends constantly to shift, mounds of sand are held in place by the mat of roots.

Storage.—The roots of many plants store food and water. Such roots may become large and fleshy, familiar examples being the sugar beet, turnip, dahlia, radish, carrot, parsnip, and sweet potato. Many plants with fleshy roots are cultivated for their roots alone and are called “root crops.” Sugar and starch are the principal forms of food stored in such roots.

Reproduction by Means of Roots.—Some plants send up stems (so-called “suckers”) from adventitious buds which arise on roots. This habit is well illustrated by the silver leaf poplar (*Populus alba*) and black locust (*Robinia pseudacacia*). Plants which normally do not produce such adventitious buds may be induced to do so by injury. In this category belong the red raspberry, some roses, and the common barberry (*Berberis vulgaris*). If the shoot of any of these is cut down at the ground line, the roots send forth new stems.

CHAPTER V

THE LEAF

THE leaf may be defined as an expanded, lateral outgrowth of the stem, arising at a node, and having a bud in its axil. The principal physiological characteristic of the leaf is its special adaptation to perform the functions of photosynthesis and transpiration. There are, however, structures such as bud scales, spines, and food-storing bulb scales, which do not perform the functions of typical leaves but which nevertheless are morphologically leaves. They are not well fitted to carry on photosynthesis and transpiration and are clearly adapted to some other special function. Because they arise at nodes or have buds in their axils, or for other reasons, these structures can be recognized as foliar (leafy) in nature.

THE ORIGIN AND DEVELOPMENT OF THE LEAF

Microscopic examination of a longitudinal section of a bud reveals each leaf originates as an outgrowth or protuberance from the primordial meristem of the growing point. (See Figs. 2 and 22.) Such an outgrowth is called a **leaf primordium**. At first its growth is chiefly apical (i.e., at the tip), but before it has reached any considerable length all of its cells begin to undergo active division and growth. From then on, growth goes on throughout the leaf. Growth of this sort, which is not restricted to the apex of the structure concerned, is called **intercalary growth**. The rudimentary leaves within the bud soon make sufficient growth in length to reach beyond the end of the growing point of the stem which, it will be recalled, lacks a special

protective cap such as is produced by the root. Overlapping one another, they form an envelope which protects the growing point of the stem from desiccation, mechanical injury, and the ill effects of too much water. In each developing bud the leaves in succession from the lowermost toward the growing point "come out" of the bud. This results from the elongation of the internodes within the bud in succession from the base of the bud upward. As each internode lengthens, the leaf or leaves at its base emerge from the bud and the bud is raised above this leaf. As soon as freed from the bud leaves resume development and quickly grow to their full size.

EXTERNAL MORPHOLOGY OF THE FOLIAGE LEAF

A typical leaf consists of three parts: (1) the expanded **leaf blade** or **lamina**, which is especially adapted for the functions of photosynthesis and transpiration; (2) the slender stalk or **petiole**, which attaches the blade to the stem and through which materials are conducted to and from the leaf; and (3) the broadened attachment to the stem, called the **leaf base**, which provides a firm attachment to the stem, in some plants partly or completely encircling it, or as in most monocotyledons, forming a long sheath surrounding the stem. Frequently there are outgrowths, sometimes similar in appearance to leaf blades, known as **stipules**, from either side of the leaf base. They are lacking in many plants, whereas in others they become detached and fall off soon after the leaves come out of the bud. Some leaves have no petioles and are said to be **sessile** (Fig. 70).

Venation.—There are two principal types of arrangement of veins: **parallel venation** and **net venation** (Fig. 72). In the former the veins that are clearly visible to the unaided eye run parallel to each other. This kind of venation is characteristic of the monocotyledons. When a parallel-veined leaf is examined with a lens it can be seen that small veinlets connect the parallel veins.

If the veins that are visible to the naked eye branch fre-



FIG. 69.—Simple leaf of pear, showing stipules.

quently and join again, so that they form a network, the leaf is said to be net-veined. The leaves of dicotyledons have this type of venation, but it rarely occurs among monocotyledons.

Net-veined leaves that have a single primary vein or midrib from which the smaller veins extend, somewhat like the divisions of a feather, are **pinnately veined**. Willows (*Salix*) offer good illustrations of this type. In other plants such as the maple (*Acer*) there may be several principal veins spreading out from the upper end of the petiole. Such a leaf is **palmately veined**.

Form of the Leaf Blade.—Leaves are said to be **simple** when, as in most plants, the blade is all in one piece (Fig. 73, *A*, *B*, and *C*). The blade of simple leaves frequently has a number of lobes separated by deep clefts



FIG. 70.—A portion of a stem of pimpernel (*Anagallis*), showing the sessile leaves.

or **sinuses**. Familiar examples of such simple **lobed leaves** are those of the oak (*Quercus*) and maple (*Acer*). The sinuses of pinnately veined, lobed leaves are always directed toward the



FIG. 71 — A branch of European linden, its leaves forming a leaf mosaic. In many plants the position taken up by the leaves of a branch or of the whole plant is such that there is very little overlapping of leaves. Thus there is relatively little shading of one leaf by another. This "mosaic" arrangement results principally from differences in the length of the petioles and curvatures of the petioles.

midrib. In such cases the leaves are said to be **pinnately lobed** (Fig. 73, *E*). Lobed leaves which are palmately veined are always **palmately lobed** (Fig. 73, *C*), the sinuses being directed



FIG. 72.—The two principal types of venation. *A*, Net venation as illustrated by the leaf of violet (*Viola*); *B*, parallel venation illustrated by the leaf of one of the bamboos. (*Arundinaria*.)

toward the base of the blade where it is attached to the petiole. Oak leaves are pinnately lobed and maple leaves palmately lobed.

In many plants, such as most ferns, the leaf blade consists of a



FIG. 73.—Common types of leaf form and venation. *A*, The simple, pinnately veined leaf of a plum (*Prunus*); *B*, the pinnately lobed, and pinnately veined leaf of an oak (*Quercus*); *C*, the palmately lobed and palmately veined leaf of a maple (*Acer*); *D*, the palmately compound leaf of wood-sorrel (*Oxalis*); *E*, the pinnately compound leaf of walnut (*Juglans*).

number of separate leaf-like parts, or **leaflets**. Such a leaf is said to be **compound** (Figs. 73, *D*, *E*, and 74). When, as in the case of the horse chestnut and clover, the leaflets are attached directly to the end of the petiole the leaves are said to be **palmately com-**

pound (Fig. 73, *D*). If the petiole is extended into a long slender structure, corresponding to the midrib of an entire leaf, and if the leaflets arise at intervals along this structure, the leaf is **pinnately compound** (Fig. 73, *E*). In the case of such leaves the slender part to which the leaflets are attached is called the **rachis**.

The edge (**margin**) of the leaf may be smooth, like that of most grasses, onion (*Allium*), and many other plants, or it may be variously toothed, as in the oak, rose, apple, cherry, etc.

ANATOMY OF THE LEAF

Microscopic examination of a typical foliage leaf shows three kinds of tissue: (1) the **epidermis**, (2) the **mesophyll**, and

(3) the vascular bundles (veins) (Figs. 76 and 78). The epidermis covers the whole leaf surface and protects the tissues within; the mesophyll is made up of parenchyma cells, most of which are green and able to carry on photosynthesis. The vascular bun-

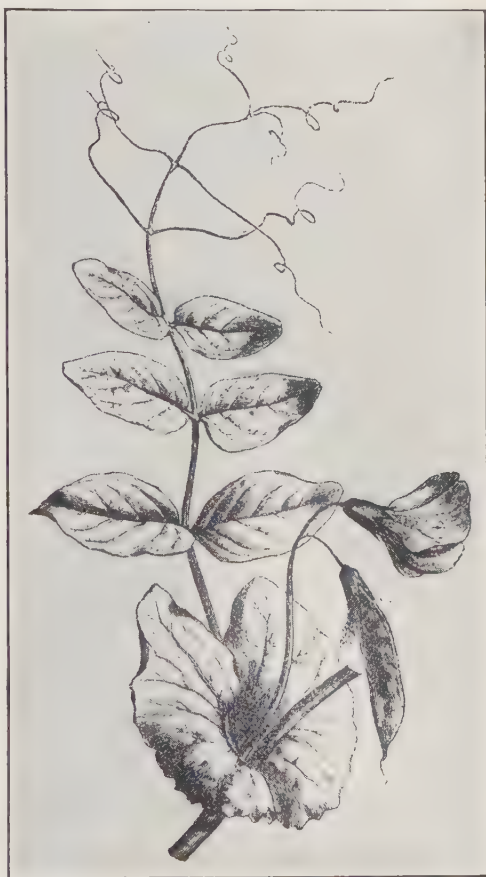


FIG. 74.—Compound leaf of garden pea (*Pisum sativum*). Note the large, leaf-like stipules, and upper leaflets, modified as tendrils. (From Bocquillon.)

dles, or veins, consist of conducting elements for the transfer of water and inorganic salts and of foods.

The Epidermis.—The total area of the leaves constitutes a very large part of the plant surface which is exposed to the air. On this account, the ability of the leaf epidermis to retard transpiration is of the utmost importance to the plant.

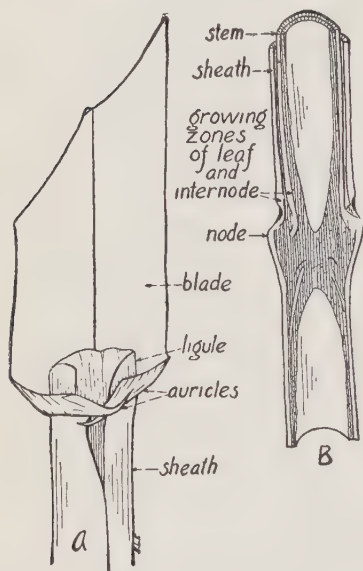


FIG. 75.—A, Portion of a leaf of barley at juncture of sheath and blade; B, stem cut in median lengthwise section. $\times 21\frac{1}{2}$. (After Robbins, from *Botany of Crop Plants*.)

When a piece of epidermis from the lower side of a leaf is examined under the microscope it is found to consist of two kinds of cells, **ordinary epidermal cells** and **guard cells**. As seen in surface view, the ordinary epidermal cells generally have a wavy outline (Fig. 77). In leaf cross sections it can be seen that the depth of the ordinary epidermal cells is considerably less than their breadth or length (Fig. 78). Chloroplasts are usually absent. The cuticle of the leaf epidermis, like that of the stem, is made up almost entirely of the waxy, waterproofing substance, **cutin**. Beneath this there may be a cellulose-cutin wall layer spoken of as the **cutinized layer**. The innermost part

of outer wall and all of the other walls of the epidermal cells are almost pure cellulose.

The protoplasts of the epidermal cells are long-lived; they do not die until just before the leaf falls. The cytoplasm forms a thin layer surrounding a large vacuole and the nucleus and nucleolus are often very conspicuous.

Guard Cells and Stomata.—Scattered among the ordinary epidermal cells of the lower epidermis, and sometimes of the

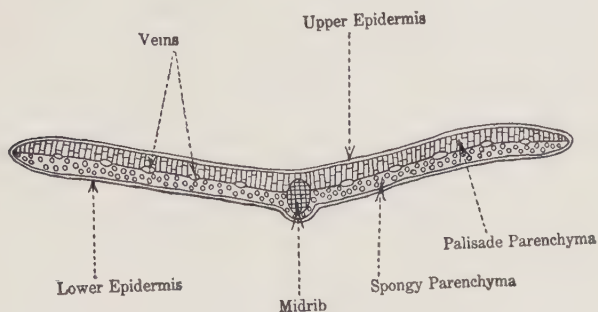


FIG. 76.—Diagram of a cross section of a common type of foliage leaf.

upper epidermis also, are the guard cells. These occur in pairs, and when seen in surface view appear broadly crescent-shaped or almost semicircular in form (Fig. 79). The more or less

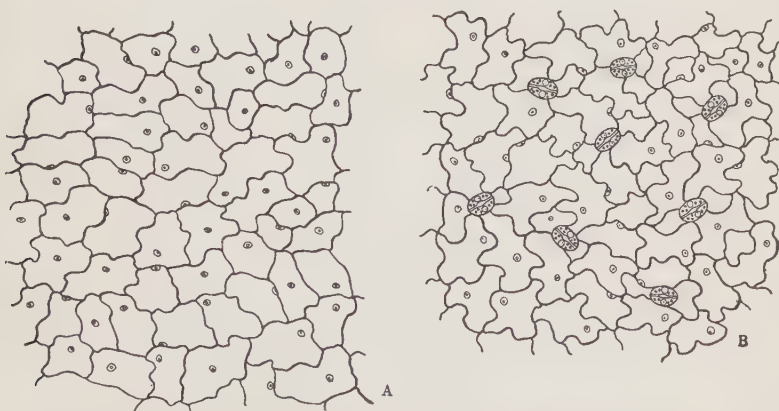


FIG. 77.—Surface view of the epidermis of a leaf of *Senecio mikanoides*. *A*, from the upper surface of the leaf; *B*, from the lower surface. The cytoplasm of the cells has not been shown.

concave sides of the guard cells are toward each other, and between them there is an opening or pore which leads from the

outside into a large air chamber in the mesophyll. This opening between the guard cells is the **stoma** (plural, **stomata**). Since the cuticle of the leaf is generally quite impermeable to oxygen,

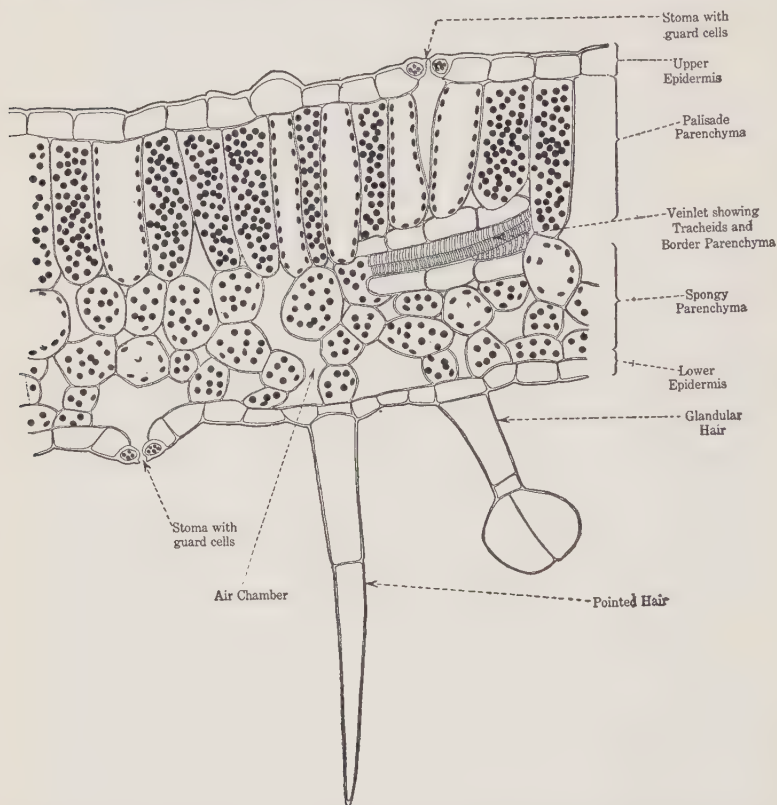


FIG. 78.—A cross section of a portion of a leaf of potato (*Solanum tuberosum*). Except for the chloroplasts none of the cell contents have been shown. Some of the cells of the palisade and spongy parenchyma have been shown in section, others in surface view.

carbon dioxide and water vapor, the passage of these three gases into or out of the leaf takes place very largely through stomata.

The guard cells have numerous, conspicuous chloroplasts. In cross sections of the leaves of many kinds of plants it can be

seen that the guard cell walls adjacent to the stoma are of greater average thickness than elsewhere. There may also be observed ridge-like outgrowths from the walls of the guard cells, which form a chamber, outside the stoma proper (Fig. 80). Sometimes the vestibule has only a narrow, slit-like opening to the outside. In xerophytic plants the ordinary epidermal cells

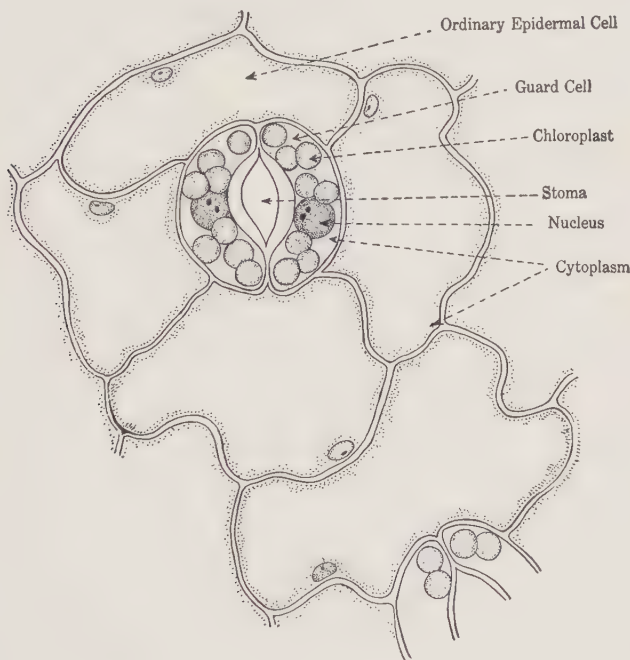


FIG. 79.—A view showing in detail a small portion of the epidermis from the upper surface of a foliage leaf.

may overlap the guard cells so that the stoma and guard cells are depressed below the general surface of the epidermis. On the other hand, plants growing in very moist habitats may have the stomata raised above the surrounding epidermal cells.

Control of Stomata by the Guard Cells.—By changes in turgor the guard cells are able to open and close stomata, thereby

regulating the entrance and exit of gases. The stomata open when the turgor of the guard cells rises; increased turgor of the guard cells is due to an increase in the concentration of their cell sap which enables them to absorb water from neighboring cells; increased concentration of the cell sap is due to an accumulation of sugar in the guard cells; sugar accumulates when the guard cells are illuminated (due to photosynthesis going on) or when a change in the acidity of the guard cell sap favors the digestion of starch to sugar. The stomata close when the turgor of the guard cells falls; decreased turgor of guard cells is due to a

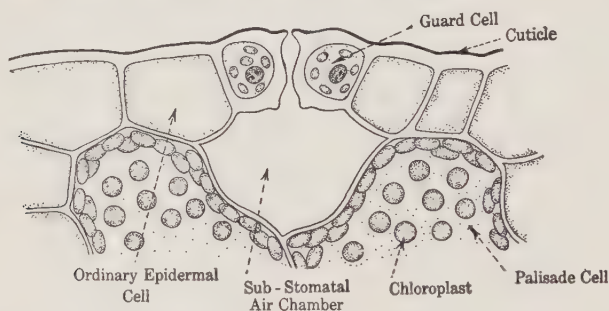


FIG. 80.—A portion of a cross section of a foliage leaf showing a stoma and a few of the neighboring cells. (Redrawn after Kny.)

decrease in the concentration of their sap which lowers their power to absorb water from adjacent cells; decreased concentration of the sap of guard cells chiefly results from the movement of sugar from them or its change to starch and the storage of the latter temporarily in the guard cells.

Epidermal Hairs.—Many leaves have hairs growing out from the epidermis. When epidermal hairs are present they are generally much more abundant on the lower than on the upper side of the leaf and frequently are restricted to the former. The simplest of these hairs are mere extensions of epidermal cells, the hair and the epidermal cell together constituting but a single cell, as in the *Cruciferae* (mustard family). Multicellular epidermal hairs, consisting of a single filament of cells which decrease

in diameter from the base to the apex, are much more common than are unicellular hairs. Branching of both unicellular and

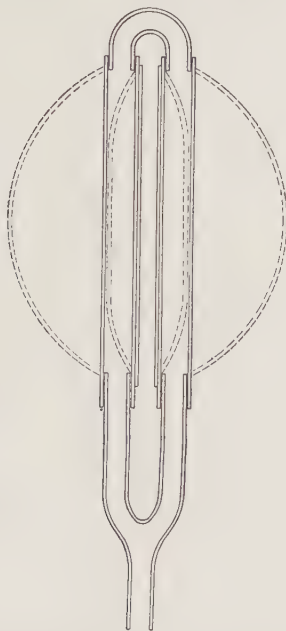


FIG. 81.—Diagram of a model illustrating the manner in which the stoma is opened when the turgor of the guard cells increases. The short glass U-tube at the base is connected to the Y-tube, also of glass, by two pieces of rubber tubing. The inner (adjacent) walls of these two pieces of tubing are made thicker than their outer walls. The thicker portions of the walls of the rubber tubing corresponds to the guard cell walls furthest from the stoma. If the water or air is forced under pressure into the Y-tube and the rubber tubing thus subjected to internal pressure, the greater extensibility of the thin, outer walls causes them to take the position shown by the outer dotted lines in the diagram. As the result of this bulging of the outer walls of the rubber tubes the inner, thick walls are drawn apart as shown. Thus, under pressure from within the tubes, the space between the tubes is widened, corresponding to the opening of the stoma. When the pressure is reduced the inner walls tend to return to their original position, narrowing the opening between them, as when the stoma is closed by the guard cells.

multicellular hairs occurs. Ethereal oils may be secreted by glandular hairs.

The Mesophyll.—The upper and lower surfaces of typical foliage leaves are usually distinctly different in appearance. The upper surface is generally darker than the lower, and the larger veins which project from the surface on the under side are, on the upper side, even with the leaf surface or depressed below it.

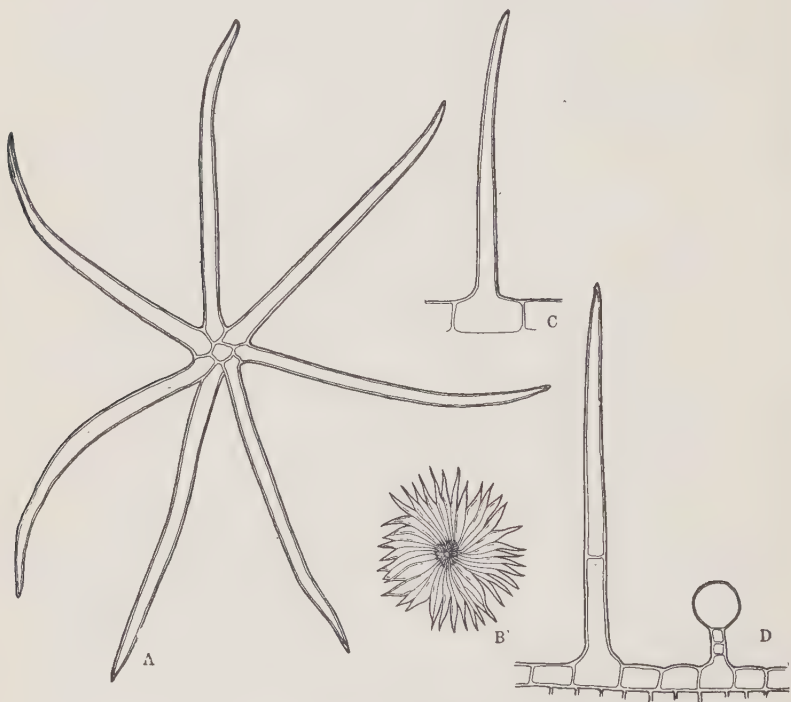


FIG. 82.—Several types of epidermal hairs. *A*, branched hair of false mallow (*Malvastrum*), this hair is attached to the leaf by a short stalk not shown in the drawing. *B*, scale-like stellate hair of *Eleagnus*, its centrally attached stalk not shown. *C*, pointed, unicellular hair of shepherd's purse (*Capsella*). *D*, a pointed multicellular and a capitate, glandular hair of geranium (*Pelargonium*).

The mesophyll is made up of three kinds of tissue: the palisade parenchyma, the spongy parenchyma, and the border parenchyma (Fig. 78).

The palisade parenchyma consists of from one to several

layers of elongated cells placed with their long axes at right angles to the leaf surface. It extends downward from the upper epidermis to the spongy parenchyma. Although this tissue is much more compact than the spongy parenchyma, intercellular spaces are by no means absent. These spaces are smaller than those of the spongy parenchyma but they are so distributed that every palisade cell is in contact with an intercellular space. Moreover, each such space communicates with the system of connecting intercellular spaces in the spongy parenchyma. Thus there is provision for the free access of carbon dioxide and oxygen to all the food-making cells of the mesophyll. On account of their position the palisade cells receive more illumination than the spongy parenchyma cells and are more abundantly provided with chloroplasts than are the latter cells.

The spongy parenchyma in most leaves forms the lower portion (generally somewhat more than half) of the mesophyll. The cells are not elongated like the palisade cells, and their form and arrangement are such that numerous large intercellular spaces exist between them. The light which reaches the spongy parenchyma cells is much less intense than that which falls upon the palisade tissue, for the former are shaded by the palisade parenchyma above them and the light which reaches them from below is, of course, much weaker than that which falls upon the upper surface of the leaf.

Border parenchyma forms a single-layered sheath surrounding the conducting elements of the veins. The cells of the border parenchyma are without chloroplasts. Although the vascular bundles of the petiole and of the large veins contain tracheal tubes, tracheids, sieve tubes, and companion cells, the finest branches of the veins are made up entirely of tracheids. At the extreme end of one of these branches the vascular bundle is in many cases reduced to a single tracheid. Most of the cells of the palisade and spongy parenchyma are some distance from the nearest sieve tube. Clearly, the tracheids which are carrying a stream of water to the food-making cells cannot well conduct the

products of photosynthesis in the opposite direction. The transfer of sugar to the nearest sieve tubes is carried on by the

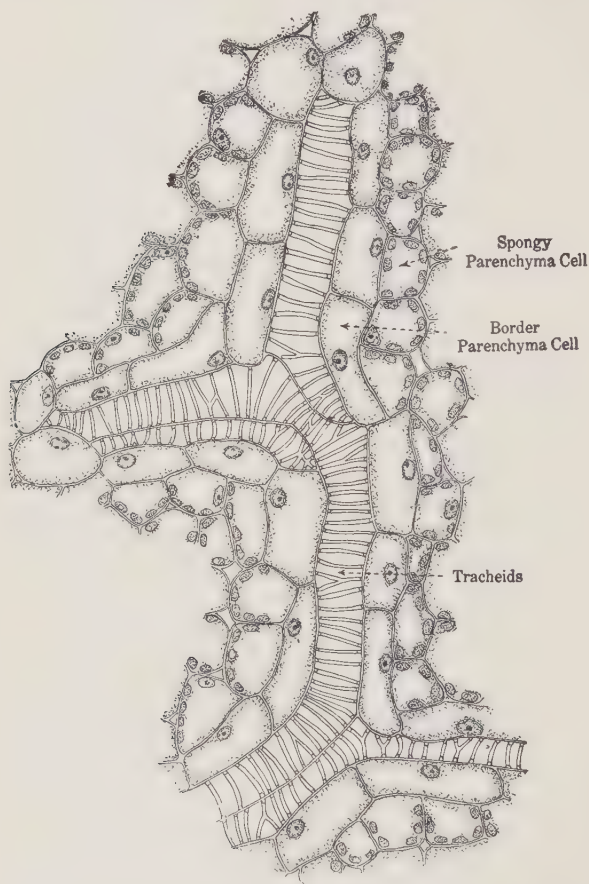


FIG. 83.—A section cut parallel to the leaf surface and through the spongy parenchyma. The free ends of several veinlets are shown as well as the relation of border parenchyma and spongy parenchyma cells to the finest veins.

border parenchyma cells. When the sugar reaches a part of the vein where there are sieve tubes, it is conducted by these elements to the larger veins, then to the midrib, and finally to the vascular

bundles of the petiole, whence it passes into the phloem of the stem.

The Vascular Bundles.—Conduction of water and of soluble carbohydrates is carried on by the veins of the leaf. When a net-veined leaf is examined with a lens it can be seen that, in addition to the veins which form the network, there are still finer branches which end free, that is, are connected to other veins only at one end. They are composed of one or a few tracheids surrounded by border parenchyma cells. The mechanical function of supporting the thin expanded sheet of epidermal and mesophyll tissue is performed principally by the large veins and the midrib.

There is no cambium in leaves and therefore there is no secondary growth of vascular bundles. Nor is there any development of cork, save that which takes place at the base of the leaf when it is shed.

Anatomy of the Petiole.—The petiole is sometimes cylindrical in form, but generally it is flattened or grooved on the upper side. The vascular bundles of the petiole are not arranged in a complete circle as in the stem, but in a semicircle or C-formed line with the opening toward the upper side of the petiole. Parenchyma and such strengthening tissues as collenchyma and bast fibers usually are present.

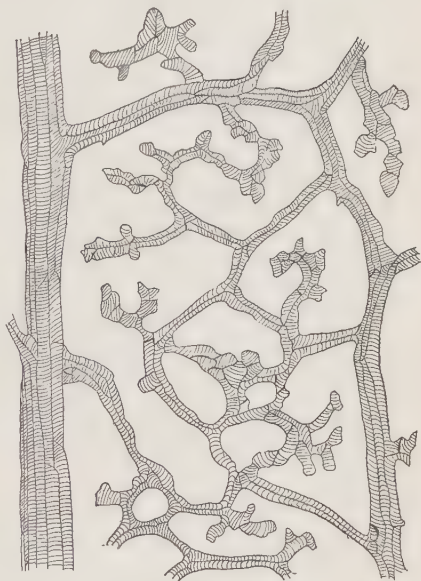


FIG. 84.—A portion of the vein system of a leaf.
(Redrawn after Sachs.)

The Absciss Layer, Leaf Fall, and Leaf Scars.—Leaf fall in deciduous plants occurs to a certain extent at all seasons but particularly at the approach of winter. The conditions which favor leaf fall cause the cells near the lower end of the leaf stalk to become meristematic and produce a zone of delicate, thin-walled cells extending clear across the base of the petiole. This is called the **absciss layer**. (See Fig. 85.) The middle lamella

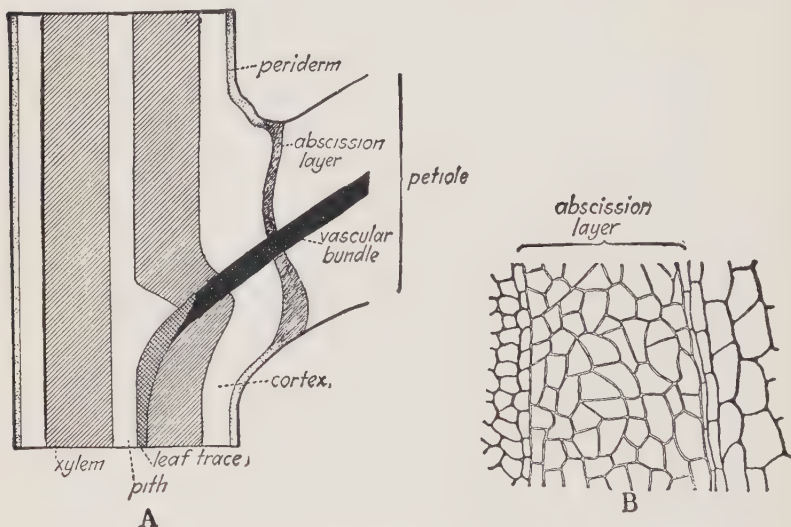


FIG. 85.—*A*, diagram showing leaf abscission layer; radial section through twig and leaf base in butternut, *Juglans cinerea*. *B*, detail of cellular structure of a small part of the layer three weeks before leaf fall. (From Eames and MacDaniels, *Introduction to Plant Anatomy*, McGraw-Hill Book Company.)

of these cells becomes changed chemically before leaf fall and when the wind blows against the blade of such a leaf the cells of the absciss layer separate from one another with ease. Certain cells just below the abscission layer become lignified and suberized and form a protective coating over the part of the stem from which the leaf has separated. These areas are known as **leaf scars**. Within each leaf scar the **bundle scars**, or broken ends

of the vascular bundles which lead from the petiole into the stem may be seen.

THE PHYSIOLOGY OF THE LEAF

The primary functions of typical leaves, for which they clearly are specially adapted in form and structure, are photosynthesis and transpiration. In certain cases, some of which will be discussed later in this chapter, leaves carry on other (secondary) functions.

Photosynthesis.—The principal factors concerned in this process of carbohydrate manufacture by green cells are as follows:

Raw Materials.—Water and carbon dioxide are the raw materials of the photosynthetic process. The soil is the source of the water and the carbon dioxide is absorbed from the atmosphere surrounding the leaves. Though the atmosphere is not absolutely constant in its composition, under natural conditions the percentage by volume of its different components seldom varies much from the following figures:

	Per Cent
Nitrogen.....	78.2
Oxygen.....	20.8
Argon.....	1.0
Carbon dioxide.....	0.03
Traces of ammonia, oxides of nitrogen, ozone, and other gases.	

Each of these gases is present, therefore, in the intercellular spaces of the chlorenchyma. If the concentration of any one of these gases in the air within the leaf increases, some of that gas will tend to diffuse outward through the stomata. If there is a decrease in concentration of any one of the gases, that gas will tend to diffuse inward through the stomata from the air outside the leaf. The surface film of water on the outside of the palisade and spongy parenchyma cells, where they are in contact with an intercellular space, as well as the cell sap of these cells, contains a quantity of each of the atmospheric gases in solution.

During photosynthesis there is a movement of carbon dioxide from the atmosphere outside the leaf to the interior of the green cells. This transfer of carbon dioxide may be considered as taking place in the following stages:

1. Passage from the outside air into the intercellular spaces, by diffusion through the stomata.

2. Solution of more carbon dioxide from the intercellular air by the film of water on the surface of the chlorenchyma cells.

3. Diffusion from the surface film, through the cell wall and cytoplasmic membrane, to the cell sap where it replaces the carbon dioxide removed from solution by photosynthesis.

The water used by the green cells enters the root from the soil and is conducted upward through the xylem of the root and stem. In the leaf it passes along the petiole, midrib, and veins to the finest veinlets. None of the green cells are more than three or four cells removed from one of these small vascular strands. Water passes from the tracheids of the veinlets to the chlorenchyma cells by reason of the much greater concentration of the cell sap in those cells than of the solution in the tracheids. But in order to do this it must first pass to the border parenchyma cells, whose cell sap is also more concentrated than the watery solution in the tracheids. From the border parenchyma cells the water then passes to the green cells because of the greater concentration of their cell sap than that of the border parenchyma cells. The process of photosynthesis tends to maintain a high concentration in the cell sap of the green cells, both on account of the sugar which it produces and because of the water which the process removes from the cell sap. However, transpiration from the green cells is probably the most important factor in maintaining a high concentration in the cell sap of these cells.

The quantity of carbon dioxide and water absorbed and converted into food and tissue by the plant is surprisingly large.

The Energy Factor—*Necessity of Light for Photosynthesis.*—There are several interesting methods of showing that carbon

dioxide and water cannot be united to form carbohydrates in the absence of light. One of these depends upon the measurement of the dry weight of a given area of leaf tissue before and after a period of active photosynthesis. The difference represents a part, but by no means all, of the material manufactured by the leaf surface in question during the day, for some of the sugar made was conducted away from the leaf and some was lost by respiration. If this experiment is repeated with plants which are kept in the dark during the day there will be no gain in dry weight. The conclusion is that light is essential to the increase in dry weight. Furthermore, it can be clearly shown that the increase in dry weight is due to the production of sugar and starch.

Further experiments show that not only is light absolutely necessary for photosynthesis, but that the process will not go on unless light actually falls directly on the green tissue. Indeed the chloroplasts themselves must be illuminated, that is, chlorophyll is essential to carbohydrate manufacture.

The Energy Factor—*The Function of Chlorophyll*.—White light is made up of ether vibrations, or waves, of different lengths, ranging from the relatively long waves of red light, through the successively shorter waves of orange, yellow, and green light to the very short waves of blue and violet light. By means of a glass prism and other devices a shaft of white light can be resolved into its component colors. In the resulting band of color, which is called the **spectrum**, the different component colors of white light are arranged in the order of their wave length. When white light falls upon a white object all the different component colors are reflected to the eye. When a white object is illuminated by red light or by blue light the object appears red or blue because of the reflection to the eye of the colored light which falls upon it.

The green color of chlorophyll indicates, at least, that this pigment reflects much of the green component of the light falling upon it, and absorbs the other kinds of light at least in

part. If we pass a ray of white light through a green leaf, of which the intercellular spaces have been filled with water to render it less opaque, the resulting spectrum will be found to be different from that of white light which has not passed through a green leaf. It will lack a considerable part of the red and much of the blue, indigo and violet. Part of the red and most of the yellow, orange, and green are only slightly changed by passage through the chlorophyll. Thus we learn that it is a certain part of the red and some of the blue, violet, and indigo

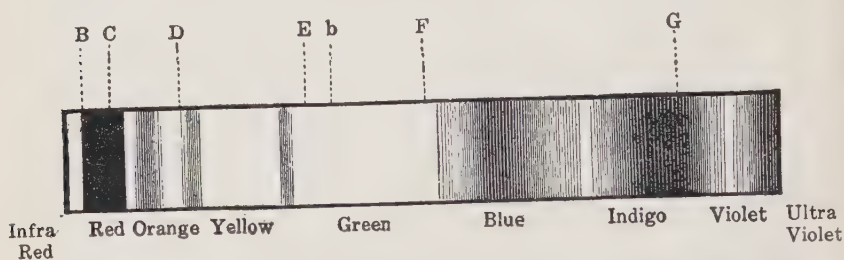


FIG. 86.—Absorption spectrum of an alcoholic extract of raw chlorophyll (chlorophyll *a* and *b*, carotin and xanthophyll) from green leaves. The letters designate the positions at which certain dark lines occur in the solar spectrum. (From Kraus.)

which are absorbed by the chlorophyll from white light as it passes through the leaf.

The Energy Factor—*Evidence of the Relative Effectiveness of Different Parts of the Spectrum.*—The production of carbohydrates from carbon dioxide and water is an energy-absorbing process, that is, a process which can go on only if energy is continuously supplied from without. Light is the only form of energy which green plants can use for this process. Now it is clear that the light which the leaf does not absorb cannot be used in photosynthesis, but it does not follow that the violet, indigo, blue, and part of the red which are absorbed are all suitable as sources of energy for that process, nor does it follow that the relatively small amounts of green, yellow, and orange light which are absorbed cannot be used in photosynthesis.

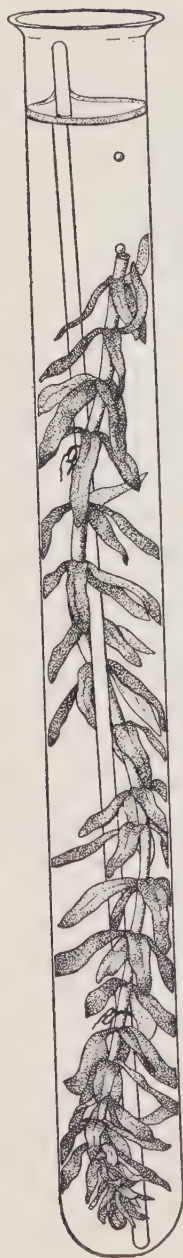
Only experiment can answer the questions as to what part of the absorbed light can be used in carbohydrate manufacture. One of the most direct methods is to project a spectrum upon a starch-free leaf which receives light from no other source, and then after a time remove the leaf from the plant and treat it with alcohol and with iodine solution. It will be found that where the orange, yellow, and green light fell upon the leaf there is little or no evidence of starch formation, but that abundant starch is present where the leaf was lighted by the blue end of the spectrum and by that portion of the red in which the absorption by chlorophyll is most complete.

Efficiency of the Leaf in Utilizing Sun's Energy.—The following table gives the principal results of one series of measurements of the efficiency of leaves in energy absorption which was made at Cambridge, England.

	Per Cent
Total energy of sunlight falling on upper leaf surface. .	100
Energy absorbed by green part of a variegated leaf. . .	80
Energy absorbed by chlorophyll-free part of such a leaf	70
Energy absorbed by the chloroplasts of green part of leaf	10
Energy actually utilized in photosynthesis.	3.5

It is clear from this table that under the conditions of this particular set of experiments about 35 per cent of the energy actually absorbed by the chloroplasts or 3.5 per cent of all the light energy falling on the leaf was used in photosynthesis. In general, the average efficiency of green plants in the utilization of sunlight falling upon their leaves is probably much less than the values given above; perhaps it is as low as 1 per cent.

The By-product.—The equation which has been used to express in simple form the chemical changes which take place during photosynthesis ($6\text{CO}_2 + 6\text{H}_2\text{O} \rightarrow \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2$) shows that oxygen is freed during the process. This gas is an incidental product or by-product of photosynthesis; its production is clearly not to be considered as the object of the process, for the green cells from which the gas is liberated are in constant and



direct contact with the intercellular air of the leaf, which normally contains a large proportion of oxygen.

Whereas photosynthesis goes on only during the period of daylight, respiration continues during both day and night. Respiration involves the absorption of oxygen and the liberation of carbon dioxide. However, in a plant which is actively growing or accumulating food reserves, the amount of oxygen liberated into the atmosphere by photosynthesis within twenty-four hours is considerably in excess of that absorbed by respiration. On the other hand, the carbon dioxide contributed to the atmosphere by the respiration of such a plant is much less than that absorbed during photosynthesis. It is important to man and to other animals that the concentration of oxygen in the atmosphere be kept fairly uniform in order that their respiration may continue at the accustomed rate. Furthermore, an accumulation of carbon dioxide in the atmosphere would sooner or later interfere with their life process. Therefore, since they are not able, as are green plants, to add oxygen to the atmosphere, or to remove carbon dioxide from it, the power of green plants to "purify" the "vitiated" atmosphere, by removing carbon dioxide from it and adding oxygen, is of considerable significance.

The End-products.—In most plants the first visible product of photosynthesis is starch. In

FIG. 87.—A branch of the immersed aquatic plant, *Elodea*, showing the liberation of bubbles of oxygen (a by-product of photosynthesis) when the plant is illuminated.

Vaucheria, one of the filamentous fresh-water algae, oil is the first product which appears, starch never being formed. It also has been reported that in many of the *Musaceae* (banana family), starch is absent from the leaves, oil again being the first visible product of photosynthesis. In many other monocotyledons there is no visible product of that process to be found within the green cells, for the sugar produced remains in solution.

The sugar which is the immediate product of photosynthesis has been generally assumed to be glucose ($C_6H_{12}O_6$). There is some evidence, however, that it may be sucrose (cane sugar) ($C_{12}H_{22}O_{11}$). Both of these sugars are present in considerable quantities in plants.

The Course of the Process.—There have been many attempts to determine the steps by which glucose or sucrose (cane sugar) is built up from carbon dioxide and water. One suggestion which has been put forward is that from the raw materials (CO_2 and H_2O) formaldehyde (CH_2O) is first formed, and that six such molecules are then built up to form a single glucose molecule ($C_6H_{12}O_6$) or that twelve formaldehyde molecules are united to form, after the loss of one water molecule, a molecule of cane sugar ($C_{12}H_{22}O_{11}$). It should be stated, however, that the question of the actual course of the chemical reactions involved in carbohydrate manufacture is still an open one.

Rate of Carbohydrate Production.—The amount of carbohydrate produced by a given area of leaf in a given time varies greatly in different plants and under different external conditions. Experiments carried out with leaves of the sunflower (*Helianthus*) show that a square meter of leaf surface may in the course of a summer's day produce as much as 25 grams of starch.

Conditions Influencing the Rate of Photosynthesis.—Under natural conditions the rate of photosynthesis is determined by three factors. These are:

1. Temperature.
2. Intensity of the illumination.
3. Carbon dioxide content of the atmosphere.

The lowest known temperature (minimum) at which it is possible for photosynthesis to go on is several degrees below the freezing-point of water. For plants of the temperate zone the optimum temperature (heat intensity most favorable) for the process is about 37° C. and the maximum (temperature above which the process ceases) from 43° to 45° .

The amount of material produced by a given area of leaf surface increases with the increase of illumination up to a certain point (the optimum light intensity) if the temperature and the carbon dioxide supply are sufficient.

Although under natural conditions optimum illumination and temperature exist for considerable periods, green leaves do not, during such periods, produce the greatest quantity of carbohydrates which they are capable of producing. The 0.03 of a per cent concentration of carbon dioxide in the atmosphere is far below the optimum. At ordinary temperatures and with moderate illumination, artificial increase of carbon dioxide up to a concentration 0.25 per cent results in increased carbohydrate production. Further increase in carbon dioxide does not increase photosynthesis unless the illumination, or the temperature, or both are increased.

Under favorable natural conditions of illumination and temperature the carbon dioxide content of the atmosphere is, then, the limiting factor for photosynthesis. That is to say, at the temperature of a sunny day during the active growing season, the amount of carbohydrate produced could not be increased by rise of temperature or increase of illumination, but only by increase of carbon dioxide concentration above that normally present in the atmosphere.

The Utilization of the Product of Photosynthesis.—The sugar, glucose, which is believed to be the immediate product of the photosynthetic process, constitutes foundation material for the synthesis of many other plant substances. Part of this carbohydrate is respired, and some of it is stored as cane sugar or starch in various tissues of the plant, but a very large portion is trans-

formed chemically into various substances which play a part in the life of the plant. We may classify these substances as follows: (1) those which compose the plant skeleton; (2) reserve foods; (3) living protoplasm; and (4) various secretions.

Part of the sugar is converted into cellulose for the formation of the walls of new cells and for the thickening of old walls of living cells. The reserve foods of which glucose forms the basis are (1) **carbohydrates** such as the sugars (fructose, sucrose, and others), starches and hemicelluloses, (2) **oils**, and (3) **proteins**.

Transpiration.—All the higher plants, except such submerged forms as water weed (*Elodea*) and water milfoil (*Myriophyllum*), constantly lose water, which passes into the atmosphere in the form of water vapor. This process is called transpiration. Though related to evaporation, such as takes place from a water surface or from a wet cloth, transpiration is different in that it is controlled in part by the plant itself. The rate of water loss (by transpiration) from a living plant is less than the water loss (by evaporation) from a dead plant.

The great surface exposed by the leaves of a typical plant is favorable to the absorption of large quantities of carbon dioxide and light energy for photosynthesis. On the other hand, it subjects the plant to the danger of transpiration exceeding water absorption, a condition which results in wilting, or, if long continued, in the death of the plant. The question naturally suggests itself as to whether the large water loss through transpiration is merely an unavoidable result of the development of a great leaf surface by the plant or is a process which likewise plays a useful rôle in the life of the plant.

Transpiration and the Transpiration Stream.—In the chapter on the Stem, the withdrawal of water from the conducting tissues of the leaf by the mesophyll cells was given as the principal factor in maintaining the stream of water and soil solutes from the root to other parts of the plant. It is this osmotic pull upon the water in the tracheids of the veinlets which is responsible for drawing upward the weak solution in the veins and

vascular bundles of the stem. The water drawn into the mesophyll cells tends to reduce the concentration of their cell sap. As a result, those cells would lose their power to take water from the veinlets and the upward stream would cease, were it not for the fact that the mesophyll cells are losing water by transpiration into the intercellular spaces of the leaf at the same time that they are withdrawing water from the veinlets. Transpiration, then, can be said to be the main condition determining the movement of water, and possibly essential minerals also, from the roots to the leaves. Although a large part of the energy of the sunlight which falls upon a green leaf is absorbed by it, a relatively small part of it is actually used in photosynthesis. The greater part of that absorbed is already in the form of heat or is transformed into heat within the leaf. As a result, temperatures very injurious or even fatal to the protoplasm might exist within the leaf during periods of exposure to very bright sunlight, were it not for the cooling effect of transpiration.

Conditions Affecting Transpiration Rate.—The amount of water lost by transpiration depends upon (1) **external factors**, conditions outside the plant, and (2) **internal factors**, conditions in the plant itself.

External Factors.—In measuring the effect of external conditions upon the rate of transpiration, the balance may be used to show, by the change of weight of a plant, the quantity of water lost.

The principal external factors which affect the transpiration rate are the following:

1. Humidity of the atmosphere.
2. Light intensity.
3. Air movements.
4. Air temperature.
5. Soil conditions.

Humidity of the Atmosphere.—The less moisture there is in the air surrounding the plant the greater will transpiration tend

to be. Though transpiration is very slight in a water-saturated atmosphere it has been shown that it does not cease entirely.

Light Intensity.—Illumination has a marked effect on water loss by transpiration. Illumination may increase transpiration in two ways: (1) by causing the guard cells to open the stomata, and (2) by raising the temperature of the leaf.

Air Movements.—When the air surrounding the plant is quiet, it becomes almost saturated with water vapor because of transpiration and the slowness with which the water vapor diffuses away from the leaf. This “moist blanket” of air naturally checks transpiration. Movement of the air sweeps away the mantle of moist air and brings fresh and drier air to the surface of the leaves; as a result transpiration increases.

Air Temperature.—Other conditions remaining constant, experiments show that in general transpiration increases with rise and decreases with lowering of the temperature of the surrounding air.

Soil Conditions.—Any soil conditions which affect the rate of water absorption will also change the rate of transpiration.

Internal Factors.—*Means of Reducing Transpiration.*—Through the layer of cuticle forming the surface of all mature leaves, some water does escape into the air. This loss of water through the cuticle is spoken of as **cuticular transpiration**, to distinguish it from water loss through the stomata or **stomatal transpiration**.

The thickening of the outer wall of the epidermal cells, the presence of large quantities of cutin on, and sometimes also in, this wall, and the production of close-set rods of wax (the so-called “bloom” which occurs on many fruits, leaves, and stems and has the appearance of a very fine powder) are the principal means by which the plant is able to reduce cuticular transpiration. The amount of cuticular transpiration is very much less than that of stomatal transpiration.

In most plants the stomata are largely or entirely confined to the lower surface of the leaves. Clearly the stomata on the under

surface of a leaf will be less likely to endanger the plant by allowing excessive transpiration than would stomata on the upper surface. The temperature of the lower, and therefore shaded, side of the leaf will be less than that of the upper side when the sun is shining brightly, and consequently the air adjacent to the lower surface of the leaf will not tend to be so dry as that next to the upper side of the leaf.

Leaves which hang straight down, like those of some poplars and the adult leaves of eucalyptus, have about the same number of stomata on the two sides. The same is true of leaves which stand almost or quite perpendicular, as in many grasses. In the case of a few plants, such as those water lilies whose leaves float on the surface of the water, there are no stomata on the lower leaf surface.

Stomatal transpiration is sometimes reduced by depression of the stomata below the general surface of the leaf. By this means the transpired water vapor is prevented from being immediately swept away from the stoma by air currents, and the rate of transpiration is thereby decreased.

Most plants, by opening or closing the stomata, are able to alter greatly and quickly the water loss due to transpiration. In general it may be said that leaves reduce water loss by closing the stomata whenever there is not necessity for carbon dioxide absorption. The guard cells generally react promptly to a change from light to darkness or from darkness to light, closing the stoma in the former case and opening it in the latter.

When water shortage begins in some plants, certain grasses for example, both stomatal and cuticular transpiration are reduced by rolling of the leaves. By this method the amount of leaf surface exposed to light and to the dry atmosphere is decreased.

It is commonly assumed that the presence of epidermal hairs reduces transpiration. Of this there is some question, especially in cases where the hairs are made up of living cells.

Many plants living in places where the water supply in the

soil is small and the atmosphere very dry appear to have reduced transpiration, both stomatal and cuticular, by having very small leaves, by shedding the leaves soon after they are formed, or by producing no leaves at all. In either of the two latter cases the stems perform the typical leaf functions.

Clearly such provisions for restricting water loss result in a great sacrifice of photosynthetic activity.



FIG. 88.—Leaf spines of common barberry (*Berberis vulgaris*). A short branch bearing ordinary foliage leaves stands in the axil of a branched spine-like leaf.

Respiration in Leaves.

—As we have already learned, the oxidation of food into carbon dioxide and water, with the liberation of the energy which was stored in the molecules of the food substance, is a process taking place in all living cells. It is particularly active in the growing parts of the plant and in the leaves and flowers. Part of the energy liberated by respiration is in the form of heat. Under natural conditions this heat



FIG. 89.—Stipular spines of black locust (*Robinia pseudacacia*).

does not cause any considerable rise in the temperature of the leaf, for it is quickly dissipated into the surrounding air.

Autumnal Coloration of Leaves.—The brilliant yellow and red tints which the leaves of deciduous trees, such as maples (*Acer*), assume some time before their fall, and which contribute so much to the beauty of the woods in autumn, are due to changes which take place in the leaf. Yellow colors result from the disorganiza-



FIG. 90.—Sundew (*Drosera*), an insectivorous plant. The leaves are covered with "tentacles" (4) each of which bears a gland at the tip from which a viscid fluid is secreted (1). Insects often come in contact with the sticky tentacles and are held, in which case neighboring tentacles bend over until they are in contact with the captured insect (3). All of the marginal tentacles may respond (2). The result is that the insect becomes engulfed in the sticky secretion and is in part digested by an enzyme contained in this secretion. It is probable that the plant is able to utilize the nitrogenous food thus secured to supplement the relatively limited supplies of inorganic nitrogen available in the soil of the particular localities in which such plants are native. (After Kerner.)

tion of chlorophyll, plastids and cytoplasm, and the red colors are due to the formation of a pigment, anthocyanin, from sugars and certain products resulting from the disintegration of chlorophyll.

Special Functions Sometimes Performed by Leaves.—Besides the primary functions of photosynthesis and transpiration, and those of growth and respiration, the leaves of various plants may perform certain special functions in the service of the whole

plant. In some cases the leaves that are adapted to carry on such special functions continue actively to transpire and to manufacture food, but in other cases their adaptation to perform a special rôle in the life of the plant is attended by loss of the primary



FIG. 91.—Pitchers of four insectivorous plants. A, *Sarracenia variolaris*. B, *Darlingtonia californica*. C, *Sarracenia laciniata*. D, *Nepenthes villosa*. Insects entering these traps are often drowned in the contained liquid. Nitrogenous material freed by their decay or through their digestion by enzymes secreted by the plant are probably absorbed and utilized by the plant. (After Kerner.)

functions. Examples of such special functions are protection (bud scales and leaf spines), food storage, water storage, attachment (tendrils), and capture of insects (insectivorous plants). The rudimentary foliage leaves of most perennial woody plants and

the other parts within the buds are protected by scale leaves called bud scales. These are generally small, brown in color, and rather tough in texture. They are often covered with dense hairs on the outer surface.

A good example of a plant in which the leaves have been transformed into protective spines is the cactus. The bulk of such bulbs as the onion (*Allium*) is made up of special food storage scale leaves. Plants of dry soil or salt-marsh habitats often have leaves much thickened and provided with a very efficient cuticle which enables them to store a great quantity of water. Leaves or leaf parts, as petioles or stipules, may be modified into tendrils. Insectivorous plants have their leaves modified in various ways to capture insects and generally have weakly developed root systems.

In the absence of leaves the leaf functions are sometimes taken over entirely by other organs, by the roots, for instance, in some tropical orchids, or by the stem as in Scotch broom and asparagus.

CHAPTER VI

THE FLOWER

Vegetative and Reproductive Functions.—Up to this point we have discussed the plant organs which are concerned primarily with the vegetative functions, i.e., with those functions through which the individual plant provides for its own needs. The function of reproduction has nothing to do with the welfare of the individual plant which carries on this function. In fact, in the case of many plants reproduction is always a forerunner of the death of the parent plant. The reproductive function, by the origin of new individuals, serves to perpetuate the species, to multiply the number of plants of the species, and to distribute the species over a larger area.

External Morphology of the Flower.—A flower is really a shoot, for it is a stem, generally a branch one, bearing leaves. The latter organs are specially adapted to carry on reproduction. For this reason floral leaves are generally very different from foliage leaves. The flower has its origin in the axil of a leaf, just as does an ordinary branch. The leaf which thus subtends a flower is ordinarily quite unlike foliage or floral leaves and is called a bract. Though really a branch, the flower differs from branches bearing foliage leaves in the following three important particulars:

1. The promeristem of this branch does not continue to grow but is completely exhausted in the formation of the floral leaves. (See Fig. 92.)

2. The floral leaves, instead of being separated by clearly perceptible internodes, are crowded together.

3. Normally there are no buds in the axils of the leaves which compose a flower.

There is a very large number of different flower forms, but with relatively few exceptions, flowers are made up of the same parts, the diversity resulting from variations in the number, form, and arrangement of these parts. In a typical flower these are (Figs. 93 and 94):

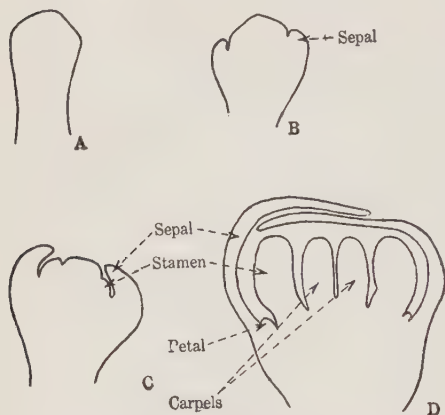


FIG. 92.—Origin and development of flower parts of shepherd's purse (*Capsella*) as shown in longitudinal sections. A, apex of the floral axis before the appearance of the primordia of any of the flower parts. B, appearance of sepals. C, the stamens have made their appearance and the carpels are just beginning to form. D, the petals have appeared and the primordia of the carpels also. Note that the latter in their formation involve all that remains of the promeristem of the floral axis. (Redrawn from Coulter and Chamberlain.)

The Essential Flower Parts:

Pistils, each consisting of

1. Ovary (basal part of the pistil which becomes the fruit).
2. Style (column of tissue arising from the top of the ovary and through which the pollen tube grows).
3. Stigma (expanded tip of style to which pollen adheres).

Stamens, each consisting of

1. Anther (the pollen-bearing body).
2. Filament (stalk or support to the anther).

The Accessory Flower Parts:

Petals (collectively called the corolla).

Sepals (collectively called the **calyx**).

The petals and sepals taken together are called the **perianth**.

Peduncle (the stalk of a flower borne singly, or that of a flower cluster or **inflorescence**. The branch stems bearing the individual flowers of a cluster are **pedicels**).

Receptacle (the broadened end of peduncle or pedicel to which the other floral parts are attached).

In a typical flower the center is occupied by the pistil or pistils; in a circle or whorl surrounding these are the stamens; outside the stamens is a circle of petals; and surrounding these a whorl of sepals.

Pistils and stamens are essential to reproduction; without the coöperation of both seed cannot be formed. Petals and sepals are not essential, but perform secondary functions; they protect the essential parts in the bud and seem to attract the insects, which in most flowers are needed to bring about seed production.

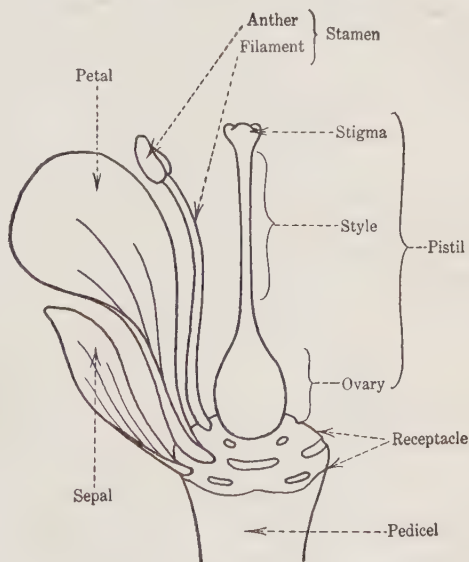


FIG. 93.—Diagram of a flower from which all but one of the flower parts of each whorl have been removed. (Modified after Hall from *A Yosemite Flora*.)

Histology of the Flower Parts.—Whereas the peduncle (or pedicel), the receptacle, and the ovary are relatively long-lived structures, the stamens, petals, and sepals are normally very

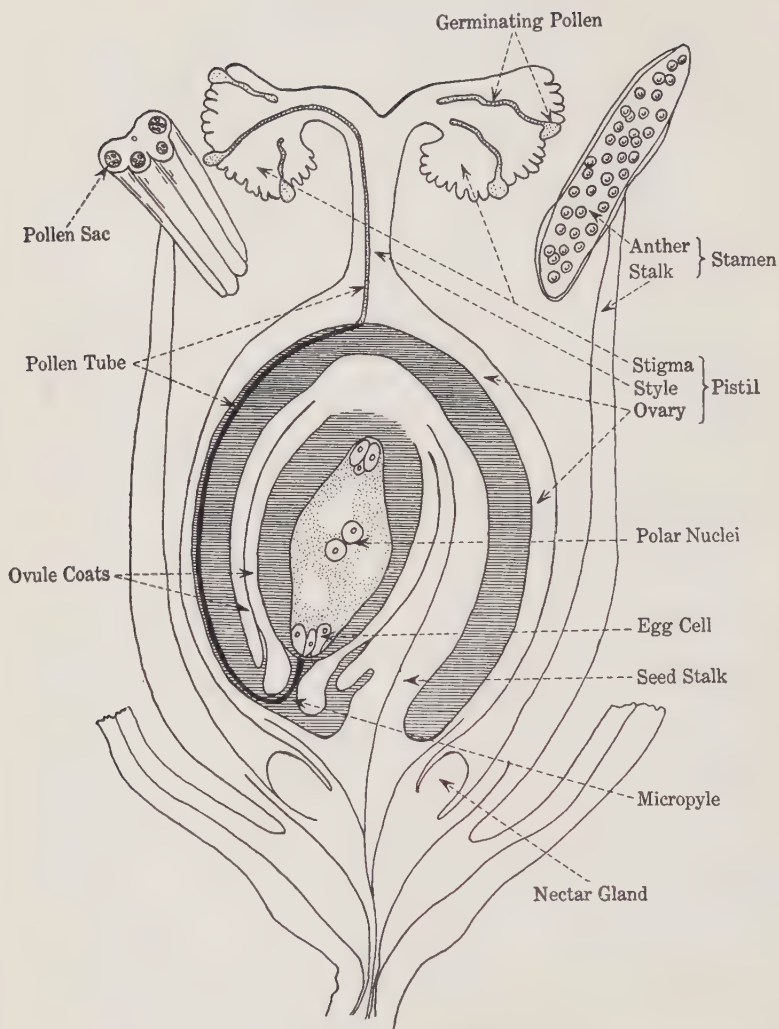


FIG. 94.—Diagram of the essential flower parts as seen in a longitudinal section of a flower. (Redrawn from Sachs.)

short-lived. Partly on account of their short life and partly because they do not perform such vegetative functions as conduction of water to other parts, food manufacture, and food storage, the stamens, petals, and sepals are much simpler in their internal structure than are the vegetative organs of the plant.

The peduncle (or pedicel) has much the same structure as an ordinary stem. In some plants the sepals closely resemble ordinary foliage leaves both in external appearance and in their anatomy. In other cases they are very similar to the petals and like them are largely made up of parenchyma cells, have a finely branched system of very small vascular bundles, and an epidermis with practically no cuticle and few, if any, stomata. Except for the cells which develop into pollen grains, the stamens are as simple in their histology as the petals, and contain even fewer bundles. The same may be said of the pistil, although the fruit into which the ovary develops generally has a well-developed epidermis, sometimes with an exceedingly thick cuticle. Chloroplasts are very generally present in the cells of the pistil and the sepals.

Sepals.—In the flower bud the petals, stamens, and pistils are usually enclosed within the calyx. This protects the parts within from mechanical injury, from rain, and from drying out. In keeping with the protective function which they serve in the bud, the sepals are generally of firmer texture than the other flower parts. However, when the petals are lacking, as in *Clematis*, the sepals, instead of being relatively small, green, and

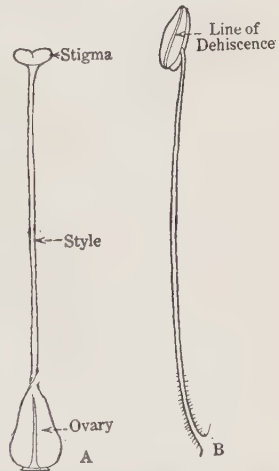


FIG. 95.—The essential flower parts of tobacco (*Nicotiana*). A, the compound carpel consisting of two carpels. B, a stamen, showing the filament (stalk) and anther.

leaf-like, may become large, delicate, and highly colored structures very similar to typical petals, and performing the function of the latter.

Petals.—In most flowers the petals probably attract insects, which may carry pollen from the stamens of one flower to the tip of the pistil (stigma) of another. This transfer of pollen from the stamen to the stigma is essential to seed formation. The petals may attract insect visitors not merely by their large size and conspicuous coloration but also by the perfume which they

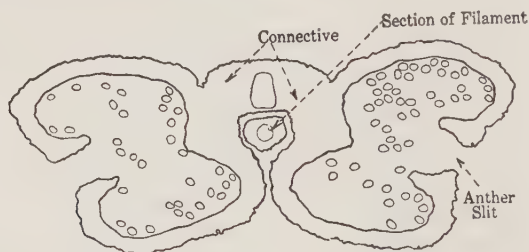


FIG. 96.—Cross section of an open anther of lily (*Lilium*). Note that the walls separating the two pollen sacs of each anther lobe (*theca*) have broken down so that but one chamber now exists in each half of the anther.

frequently produce, and in many cases by the sweet product (nectar) of sugar-secreting glands or **nectaries** (Fig. 94).

The color of the petals may be due (1) to pigments dissolved in the sap of their cells, (2) to pigments contained in the plastids, or (3) to the combined effect of both kinds of pigmentation.

Stamens.—The stamen consists of a **filament** and an **anther**. The filament serves merely to support the anther, while the latter performs the essential function of the stamen, which is pollen production. The anther consists of two **lobes**, elongated in a longitudinal direction, and united by a band of tissue called the **connective**. If an unripe anther is cut crosswise it can be seen that each lobe contains two cavities, or **pollen sacs**, within which the pollen grains are produced (Figs. 95 and 96). When the pollen is ready to be shed, these open, generally by longitudinal slits.

Pistils.—When a pistil consists of a single modified leaf or carpel, it is spoken of as a **simple pistil**; when it is composed of several carpels, as is more commonly the case, it is a **compound pistil**.

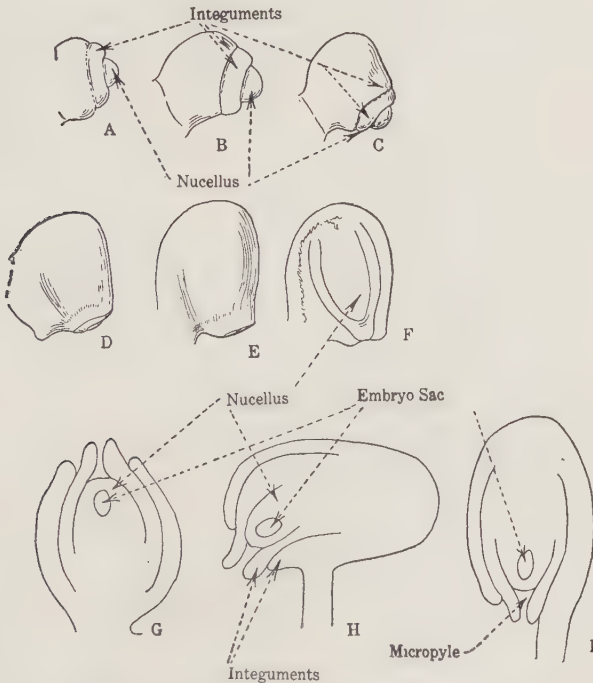


FIG. 97.—A–F, stages in the development of an ovule; G–I, three types of ovules differing in the attachment to the stalk or funiculus. (A–F, redrawn from Gray; G–I, redrawn from Prantl in Engler and Prantl's *Nat. Pflanzenfam.*)

Whether the pistil be simple or compound it almost always has three parts: (1) an enlarged basal part called the **ovary**, which is just above the attachment to the receptacle; (2) a column of tissue arising from the top of the ovary and called the **style**; and (3) a more or less expanded part at the upper end of the style, called the **stigma**. The stigma commonly has its surface roughened by short, cellular protuberances, and generally secretes

a sweet and sticky solution, the **stigmatic fluid**. In wind-pollinated plants (grasses, e.g.) the stigma often is much branched. The style may be very short or even lacking, or long and fila-

mentous. The styles (corn silk) of Indian corn (*Zea mays*), illustrate the latter extreme.

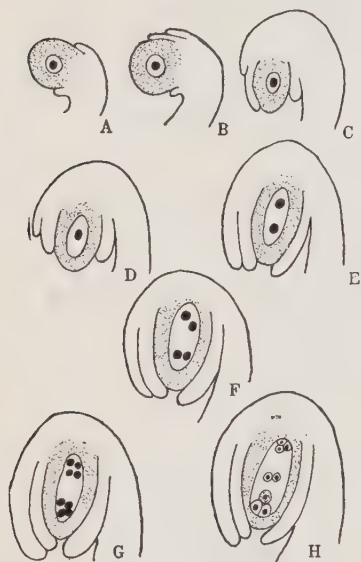


FIG. 98.—Stages in the development of the ovule of *Lilium* (lily) as seen in longitudinal sections. A, inner integuments beginning to grow up around the nucellus. B, outer integuments are appearing. The continued growth of these integuments is shown in the figures which follow (C-H). (Redrawn from Gager.)

The regions within the ovary to which the **ovules** (rudimentary seeds) are attached are called **placentae** (singular, **placenta**). In most flowers the number of placentae is the same as the number of carpels in the pistil and in such cases the placentae generally correspond quite evidently to the in-rolled and united edges of the carpels. If the placentae are on the ovary wall, as in the currant and gooseberry (*Ribes*), they are said to be **parietal**. If they are borne on the axis of an ovary which has several locules (compartments), as in lilies (*Lilium*), they are said to be **axile**. Of much less frequent occurrence than parietal or axile placentation is **free central** placentation,

in which the ovules are borne on the axis of a unilocular ovary (ovary with but one locule). This type of placentation occurs in the primrose family (*Primulaceae*).

Figure 98 shows a series of stages in the development of an ovule. The ovule first appears as a slight protuberance upon the surface of the placenta. This protuberance develops into a stalked mass of tissue with the free end (the **nucellus**) rounded.

From the base of the nucellus there later arise two rings of tissue which grow up around the nucellus and enclose it except for a narrow pore at the end. These two layers of tissue are called the **inner integument** and the **outer integument**. The pore leading from the outer surface of the ovule between the edges of the two integuments down to the surface of the nucellus is called the

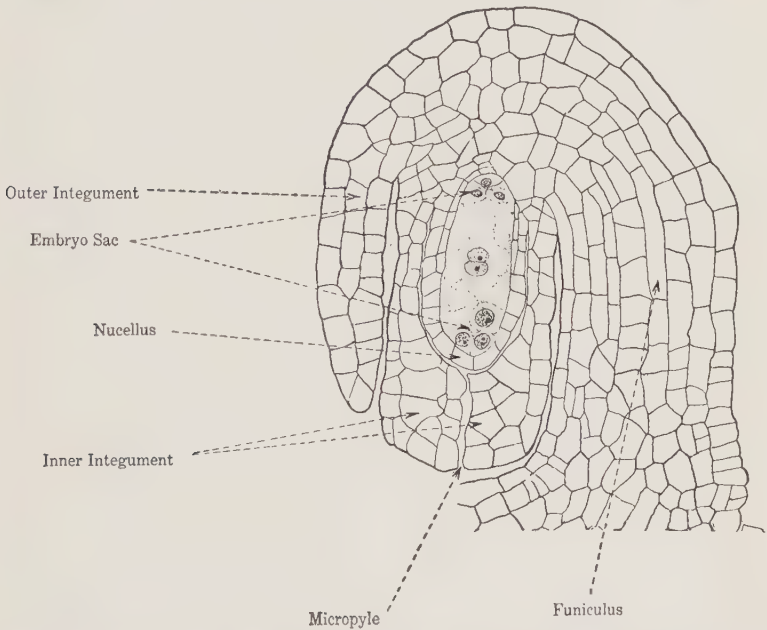


FIG. 99.—Longitudinal section of a lily (*Lilium*) ovule showing the embryo sac ready for fertilization. At the end of the embryo sac nearest to the micropyle are the two synergids and the egg cell; at the opposite end are the antipodal cells and in the center are the polar nuclei.

micropyle. Buried in the tissue of the nucellus in a mature and fully developed ovule is the **embryo sac**, a structure of great importance in the process of sexual reproduction whereby the ovules become transformed into seeds. Figures 94 and 99 show fully developed ovules in longitudinal section. In these it can be seen that the embryo sac consists of a mass of vacuolated cyto-

plasm with eight nuclei lying free in it. The two nuclei at the micropylar end of the embryo sac are the so-called **synergids**; near them is the **egg nucleus**. At the opposite extremity of the embryo sac are also three nuclei, termed the **antipodal nuclei**. In many plants each of these nuclei, together with a little cytoplasm, becomes surrounded by a cell wall; in such cases they can best be spoken of as antipodal cells. Between the egg nucleus and the antipodal nuclei there are two nuclei which lie close together or in actual contact. These are the **polar nuclei**.

Absence of Certain Parts.—A great many species of plants have flowers which are lacking in one or more of the four kinds of parts present in typical flowers. In many such **incomplete** flowers the perianth (sepals and petals) is absent, in other cases the calyx is present but the corolla is lacking, and in still other incomplete flowers it is one or the other of the essential flower parts (stamens or carpels) which is not present.

The absence of the perianth or its reduction to mere scales or hairs is characteristic of the flowers of such monocotyledons as the grains and grasses (*Gramineae*) (Fig. 100). With very few exceptions, flowers that have no perianth are wind-pollinated.

Many of the flowers which have sepals but lack petals are inconspicuous and apparently not fitted to attract insects, as in the nettle family (*Urticaceae*); but in other cases, such as Clematis and Dutchman's pipe (*Aristolochia*), the sepals, by virtue of size and either conspicuous coloration or shape, take the place of the petals in relation to insect pollination.

Some plant species bear no flowers that have both stamens and carpels. It is clear that in such cases there must be two kinds of incomplete flowers if seed production is to be accomplished, namely, stamen-bearing or **staminate** flowers and pistil-bearing or **pistillate** flowers. Such flowers are called **imperfect** to distinguish them from the **hermaphrodite** or **perfect** flowers (flowers with both stamens and carpels) borne by most plants.

In some cases both staminate and pistillate flowers occur upon each individual plant in the species. Such plants are said to be



FIG. 100.—Common oats (*Avena sativa*). (Right), the inflorescence, a panicle. (Upper left), a single spikelet; *b*, pedicel; *c*, lower empty glume; *d*, upper empty glume; *e*, lemma with dorsal awn (*f*); *g*, sterile flower. (Lower left), a single flower; *h*, rachilla; *i*, palea; *j*, lodicules; *k*, anther; *l*, ovary; *m*, plumose stigma. (After Jepson, from *Flora of Economic Plants*.)

monoecious. This is the case in Indian corn or maize (*Zea mays*) where the tassel is a group of staminate flowers and the young ear a group of pistillate flowers. When the pistillate flowers are produced by one individual plant and the staminate by another, the species is spoken of as **dioecious**. In such cases there will be no seed production unless at least two individuals (a staminate and a pistillate plant) are growing close enough for the pollen to be transferred. There are relatively few dioecious species. Some of the most familiar are the date palm (*Phoenix dactylifera*) and asparagus.

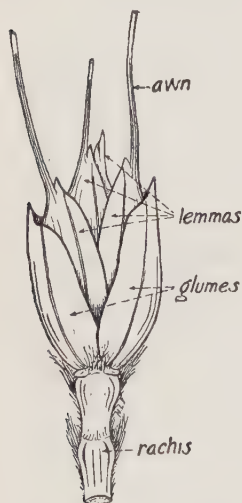


FIG. 101.—A single spikelet of wheat (*Triticum*). After Robbins, from *Botany of Crop Plants*.

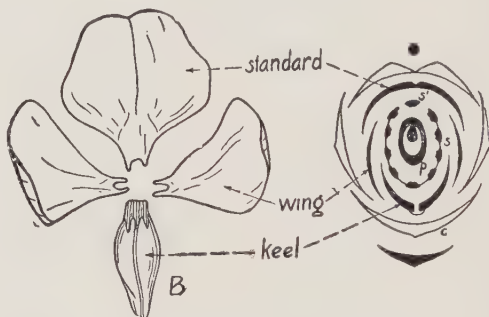


FIG. 102.—Bilaterally symmetrical flower of a legume (*Leguminosae*). A, floral diagram of horse bean (*Vicia faba*). B, corolla of a sweet pea flower (*Lathyrus odoratus*), dissected, diagrammatic. (A, after Eichler, B, after Bergen.)

There are many cases where, in addition to pistillate and staminate flowers, a species also bears perfect (hermaphrodite) flowers. These species are described as **polygamous**. Examples of such plants are certain maples (*Acer*), and some species of ash (*Fraxinus*).

Form and Arrangement of Parts.—The majority of flowers are typically star-shaped, that is, they have a corolla composed of similarly shaped and equally spaced petals which radiate out

from the center of the flower. Flowers of this type almost always have a similar arrangement of the other flower parts and are usually regular flowers in that all the members of each whorl are of the same form.

Such a condition in a flower or any other structure is often spoken of as **radial symmetry**. There are, however, many flowers

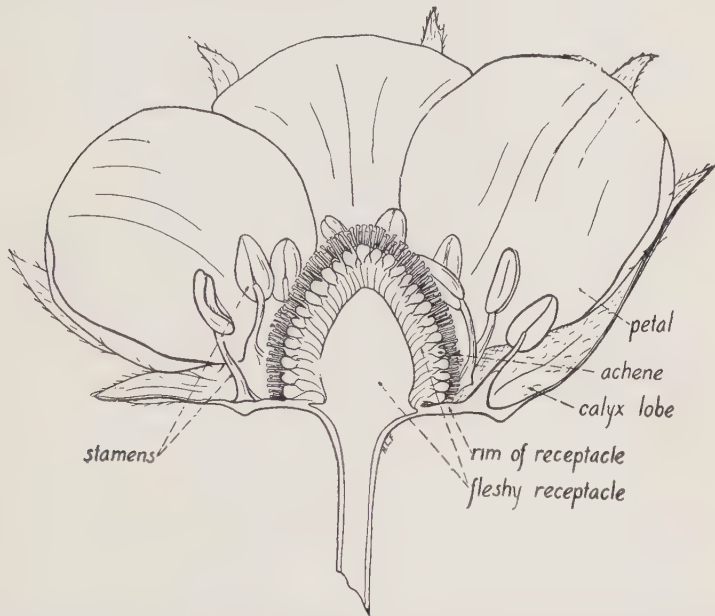


FIG. 103.—Median longitudinal section of the flower of strawberry (*Fragaria*) showing the numerous separate carpels attached to a common receptacle. (After Robbins, from *Botany of Crop Plants*.)

which are not “star-shaped” and generally in these one or more members of at least one whorl are of different form from the other members of the same whorl. Among the most familiar examples of such **irregular** flowers are the blossoms of peas, beans, and most other *Leguminosae* (Fig. 102), and of violet. Flowers such as these do not have radial symmetry but at the most, **bilateral symmetry**, which is to say that there is only one plane along

which they can be cut into halves that are mirrored images of each other.

Union of Flower Parts.—In most flowers, instead of all the parts being free and separate down to their attachment to the

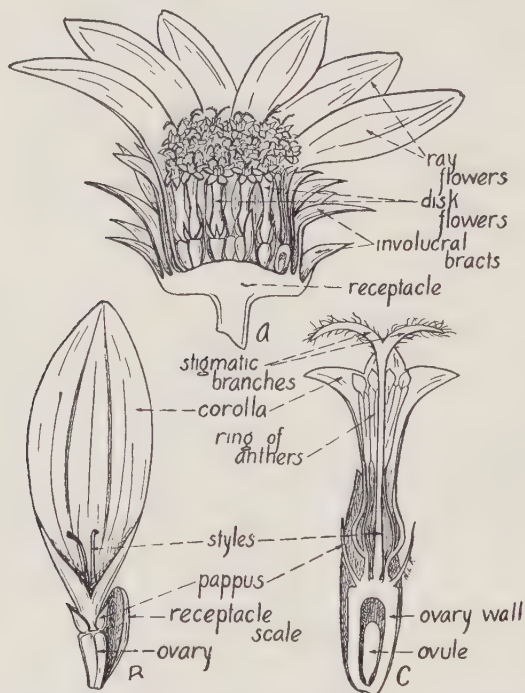


FIG. 104.—Jerusalem artichoke (*Helianthus tuberosus*). A, longitudinal section of the head (inflorescence), showing the numerous separate flowers attached to a common receptacle. B, a single ray flower. C, a single disk flower, cut lengthwise. (After Robbins, from *Botany of Crop Plants*.)

receptacle, those of one or more whorls are to some extent united with each other or to the members of other whorls.

Most flowers which possess several carpels have the carpels more or less united. In some instances, however, as in strawberry (*Fragaria*) (Fig. 103) and raspberry and blackberry (*Rubus*), the flowers have numerous carpels which are not united.

In the flowers of beans and peas and many related plants nine of the ten stamens, or in some cases all ten, have their filaments united into a sheath which surrounds the pistil, but the anthers are free. On the other hand, in the sunflower family (*Compositae*) the anthers are united and form a tube around the pistil while the filaments are free. There are many other flowers in which there is a union of the stamens.

In many flowers the members of one or both perianth whorls are united along the edges with other members of the same

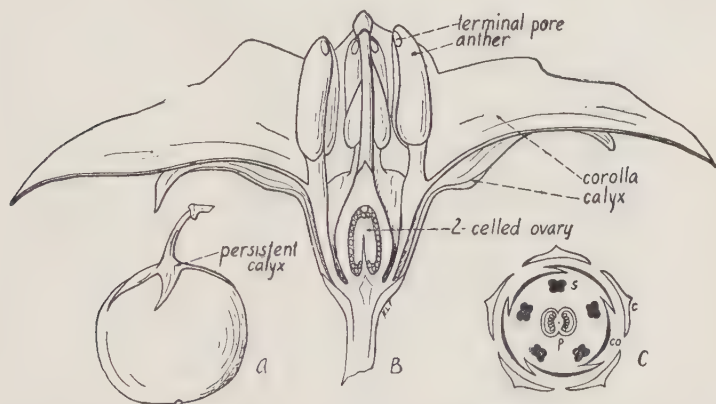


FIG. 105.—Flower and fruit of potato (*Solanum tuberosum*). A, mature fruit, a berry. B, median lengthwise section of the flower. C, floral diagram. Note that the stamens are attached to the corolla which consists of petals united along their edges. (After Robbins, from *Botany of Crop Plants*.)

whorl. There are many familiar flowers which show distinctly a more or less complete union of the petals.

Occasionally there is union between members of different whorls. Not infrequently stamens are united at their bases to the petals, and in some rare cases stamens and carpels join.

Hypogyny, Perigyny, and Epigyny.—(Fig. 106). When the receptacle is convex or conical, the whorls of flower parts are situated one above another and in the following order, beginning with the lowest: sepals, petals, stamens, and carpels. Such a

flower is said to be hypogynous. When the receptacle spreads out into a more or less deeply concave structure, at the center of which the pistil is attached, and at the margins or around the summit of which the sepals, petals, and stamens have their origin, these parts seem to be attached around instead of below the ovary, and the flower is called perigynous. The ovary of a perigynous or hypogynous flower is spoken of as superior. If the

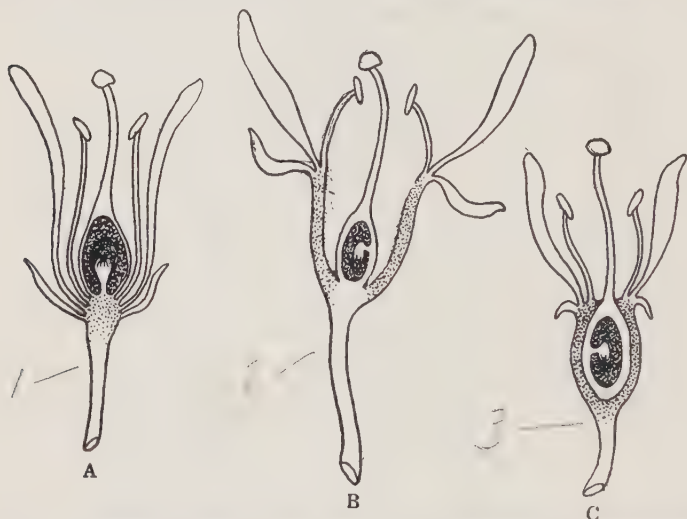


FIG. 106.—Diagrams showing the structure of (A) hypogynous, (B) perigynous and (C) epigynous flowers.

concave receptacle not only surrounds the ovary but is fused with it, the other flower parts appear to arise from the top of the ovary. This type of flower is epigynous, and its ovary is inferior. The fruits formed by epigynous flowers often bear at the unattached end the withered remains of the sepals and the stamens, or of other flower parts. The raspberry (*Rubus*) and the strawberry (*Fragaria*) have hypogynous flowers; the cherry, peach, and plum (species of the genus *Prunus*) (Fig. 107) have perigynous flowers; and the apple and pear (two species of the genus *Pyrus*) have epigynous flowers.

THE REPRODUCTIVE PROCESSES OF FLOWERS

Pollination.—As was stated earlier in this chapter the anthers of the stamens open when the pollen is mature and the pollen grains escape. In grass flowers and other flowers whose pollen is carried by the wind the anthers are attached to the filaments in

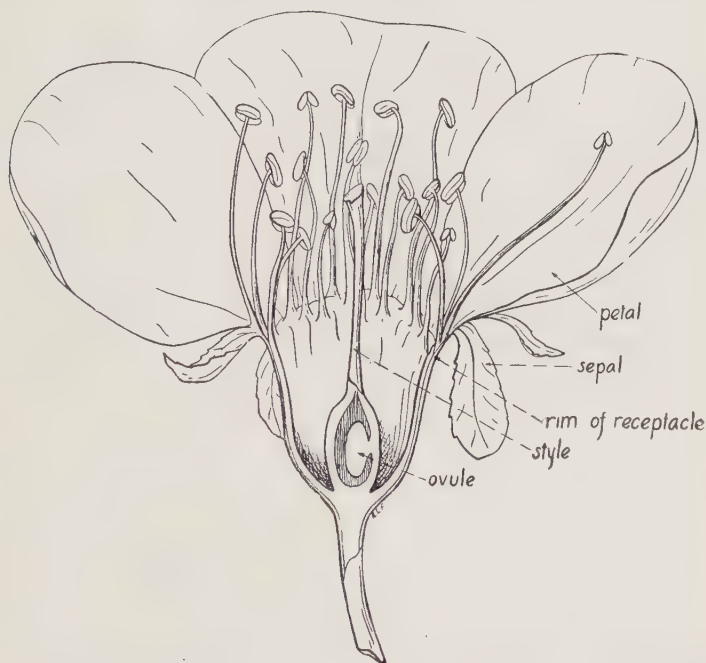


FIG. 107.—Perigynous flower of sour cherry (*Prunus cerasus*), in median length-wise section. (After Robbins, from *Botany of Crop Plants*.)

such a manner that air movements easily swing them back and forth. As a result the pollen falls from the anthers and is launched into the air. The pollen grains, being small and light, may be carried considerable distances by a slight breeze. Thus some of the pollen grains, although relatively few compared to the great number which are lost and never function, reach the stigmas of

flowers of the same species. The stigmas of such species generally are much branched and plume-like, so the chances of pollen coming into contact with them is greater than would otherwise be the case. The transfer of pollen from the anther to the stigma is called **pollination**. In some plants the pollen is borne by the wind. In a few cases water and birds are the agencies of pollination. In the majority of flowering plants, however, pollen transfer is accomplished by bees (which visit the open flowers to secure

nectar for the making of honey or to get pollen for the feeding of the young bees in the hive) or by other insects. Such plants are said to be **insect-pollinated**. In insect-pollinated plants, the pollen does not fall from the opened anthers but sticks to the outside of the shrunk anthers until swept off by contact with the



FIG. 108.—Pollen grains of various forms and markings. (After Kerner.)

body of a visiting insect. When the insect visits another flower some of the pollen which has adhered to its body may be rubbed off on the stigma.

The mature pollen grain at the time it is discharged from the anther is a spherical or oval cell equipped with two surrounding membranes, of which the inner is called the **intine** and the outer the **exine**. About the time the pollen grain is shed the single nucleus generally divides into two, the **generative nucleus** and the **tube nucleus** (Figs. 109 and 229). These are not separated by a cell wall, but the cytoplasm surrounding the generative nucleus is generally distinctly differentiated from the rest of the cytoplasm of the pollen grain.

Formation of the Pollen Tube.—Pollen which has reached the stigma adheres there by reason of the fact that the stigmatic surface consists of short outgrowths, or papillae. In many plants these are covered by a sticky secretion, the **stigmatic fluid**. Soon after pollination the protoplasm absorbs water and swells, breaking the exine. The intine is stretched and extends through the

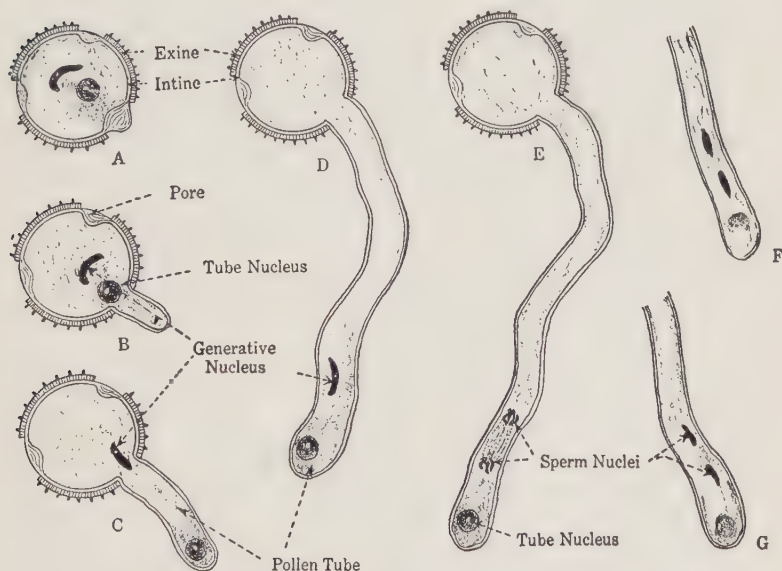


FIG. 109.—Stages in the germination of the pollen grain, and development of the pollen tube. Diagrammatic. (Redrawn from Bonnier and Sablon.)

break in the outer wall as the limiting membrane of a protoplasm-lined tube. This **pollen tube** penetrates the tissue of the stigma, grows down through the style and enters the ovary. As the styles of most flowers are not hollow, this passage necessitates the secretion of tissue-dissolving enzymes by the tip of the advancing tube. During the growth of the pollen tube the generative nucleus undergoes division, forming two nuclei, the so-called **sperm nuclei** or **male nuclei**. The two male nuclei and the

tube nucleus, together with most of the cytoplasm, pass to the tip of the tube and remain there as the tube advances.

Fertilization.—The structure of the ovule and the embryo sac within it has already been described (pages 141 and 142). It will be recalled that the fully developed embryo sac consists of a vacuolated mass of cytoplasm containing eight nuclei: three antipodal nuclei, two polar nuclei, two synergids, and one egg nucleus (Figs. 94 and 99).

When the pollen tube reaches the ovary it grows toward one of the ovules and enters the embryo sac, generally through the micropyle and nucellus. In some species, however, it reaches the embryo sac by piercing either the integuments or the base of the ovule. After entering the embryo sac the wall at the tip of the pollen tube breaks and the three nuclei, along with some cytoplasm, are discharged into the sac (Fig. 232). One of the sperm nuclei moves toward the egg nucleus and fuses with it. The fusion nucleus or fertilized egg nucleus and associated cytoplasm is called the **zygote**. The second male nucleus passes to the center of the sac, where it unites with the polar nuclei, or, in case these have previously combined, with the single resultant nucleus. The nucleus thus produced by the fusion of the three nuclei is called the **primary endosperm nucleus**.

The union of the egg nucleus with one of the male nuclei and of the polar nuclei with the other is spoken of as **double fertilization**.

Formation of the Embryo.—Shortly after the fertilization of the egg nucleus, the fusion nucleus, together with some of the cytoplasm of the sac, becomes surrounded by a cell wall. By a series of cell divisions it ultimately gives rise to the rudimentary plant or embryo of the seed, further development of which produces the mature plant. Figure 110 shows a number of stages in the development of the embryo from the zygote.

Fate of the Synergids and Antipodal Nuclei.—In many plants one or both of the synergids are destroyed by the pollen tube as it enters the embryo sac. The antipodal nuclei may persist for

some time, but sooner or later, along with any remaining synergids, they undergo disorganization, and the protoplasm is utilized as food for development of endosperm or embryo.

Formation of the Endosperm.—Shortly after fertilization the primary endosperm nucleus undergoes repeated divisions

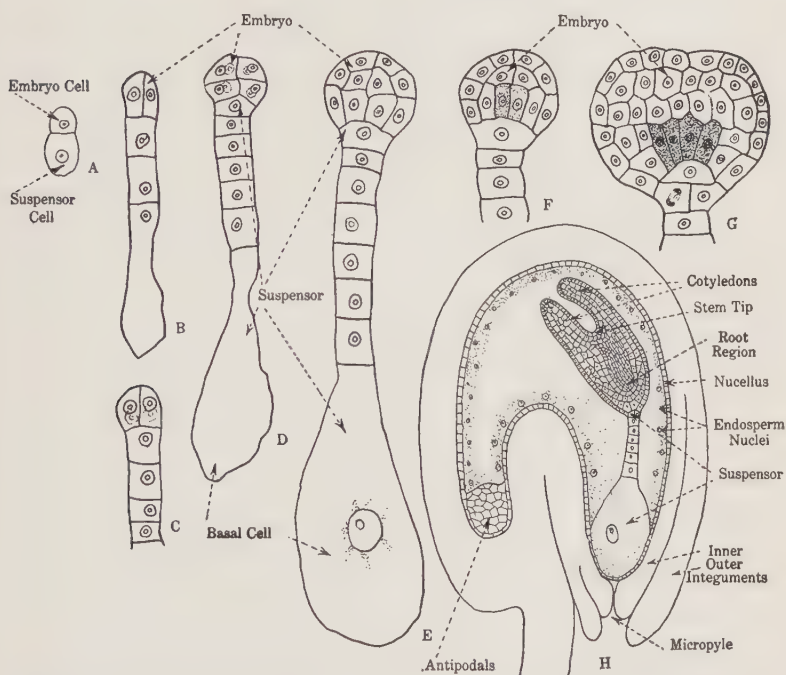


FIG. 110.—Stages in the development of the embryo of shepherd's purse (*Capsella*) a dicotyledonous plant. (A–G, redrawn from Coulter and Chamberlain; H, redrawn from Bergen and Caldwell.)

which are not attended by the immediate formation of cell walls. The cytoplasm of the embryo sac meanwhile increases in amount as food is supplied from the surrounding tissue of the ovule. The numerous endosperm nuclei and this cytoplasm come to line the embryo sac and finally may fill the whole sac, except for the space occupied by the developing embryo. Sooner or later

there is an almost simultaneous formation of cell walls between all the endosperm nuclei resulting in a mass of tissue called the **endosperm**.

Further Development of the Seed.—Fertilization stimulates the tissues outside the embryo sac to active growth so that the whole ovule increases greatly in size. Thus the seed may grow to be hundreds of times as large as the unfertilized ovule. In addition to increasing in number, the cells of one or both integuments of the ovule undergo great changes in the nature and thickness of their cell walls, and thus the **seed coats** are formed. The nucellus in most cases does not take any part in the development of the seed after fertilization but practically disappears through compression or absorption of its cells before the seed is fully developed. The endosperm grows actively for a longer or shorter period of time depending on the species. Similarly the length of time it remains after completing its development varies. In some plants, such as the bean (*Phaseolus*), pea (*Pisum*), and other legumes, the material of the endosperm is entirely consumed by the embryo before the seed ripens. In such cases the mature seed consists only of an embryo and one or more seed coats. In other species (all grasses, for example) much of the endosperm remains even in the ripe seed. It is then available as a source of food for the embryo during germination.

Effect of Fertilization on Fruit Formation.—The effect of fertilization generally extends to the ovary and starts growth and differentiation of its cells, resulting in fruit formation. In the apple, pear, and several related plants, the receptacle is also stimulated to growth and takes part in the formation of the fruit. There are, however, many plants in which the stimulation of fertilization is not essential to fruit production.

CHAPTER VII

FRUIT AND SEED

THE FRUIT

ALTHOUGH such stems as sugar cane and the Irish potato tuber, and such roots as those of the sugar beet, sweet potato, and carrot are important elements in our diet, there can be no doubt that fruits and the seeds which they contain are, of all plant parts, the most important as food sources.

In the botanical sense, a fruit is the matured ovary of a flower, including its one or more seeds (matured ovules), and any other part of the flower which is not shed after fertilization and is closely associated with the matured ovary. This definition would include such one-seeded, dry fruits as corn, oats, wheat, rice, and other cereals, which are commonly spoken of as seeds, as well as tomatoes, the pods of beans and peas, walnuts, acorns, and many other structures which are not fruits in the popular sense.

Our present-day fruits, in all their variety, have been derived from wild plants which in their primitive state yielded fruits of inferior quality.

The Development of the Fruit.—The stimulus of fertilization, the nature of which is not well understood, extends its influence not only to the ovule (which develops into the seed), but to the rest of the ovary as well, and in some cases beyond the ovary to include tissue of other flower parts. In the great majority of plants fruit does not form unless pollination is followed by fertilization and this by normal seed development.

In most fruits the following correlation seems to exist; that

the greater the number of seeds present, the larger the size of the fruit, the heavier the flesh, and the richer the content of sugar and acid.

Fruit development sometimes occurs in the absence of fertilization, and is known as **parthenocarp**y, such fruits being practically always seedless. Examples are: seedless raisin grapes, navel oranges, bananas, and pineapples. Very rarely, however, seeds may develop parthenogenetically (without fertilization) in parthenocarpic fruits. Moreover, not all seedless fruits are parthenocarpic, for seedlessness may be due to abortion of the embryos after fertilization rather than to absence of fertilization.

Structurally, the ovary walls are relatively simple, being largely made up of parenchyma cells, but the structure of the fruit wall or pericarp, into which they develop is sometimes quite complex, three distinct layers often being present. The outermost layer, the exocarp, usually consists of a single layer of cells, constituting the epidermis. The mesocarp (middle layer) is a very thin layer in some fruits, and as much as several centimeters thick in others. The endocarp (inner layer) may consist of a single layer of cells or a number of cell layers (modified in one of a number of different ways).

TYPES OF FRUITS

Simple Fruits.—The fruits of the great majority of flowering plants are simple fruits, each arising from a single ovary. These simple fruits may have the pericarp fleshy and so be known as **fleshy** fruits, or they may have the pericarp dry, and be **dry** fruits.

There are three principal types of fleshy fruits:

1. The **berry** (fruit with fleshy ovary walls enclosing one to many seeds) as the grape, gooseberry, pepper, tomato, date, and some hard or leathery-rind fruits such as squash, cucumber, orange, and lemon.

2. The **drupe** or **stone fruits**, as the cherry, peach, almond, plum, and olive.

3. The **pome** (core fruits), as pear, apple, and quince.

The dry fruits are classified into those which open when ripe—the **dehiscent** fruits, and those which do not open when ripe—



FIG. 111.—Fruits of common plants, illustrating, with the exception of *f*, the principal methods of dehiscence. *A*, pod of pea (*Pisum sativum*). *B*, silique of mustard (*Brassica*). *C*, capsule of Jimson weed (*Datura*), septicidal dehiscence. *D*, three follicles of larkspur (*Delphinium*). *E*, samara of maple (*Acer*). *F*, aggregate fruit of raspberry (*Rubus*). *G*, capsule of violet (*Viola*), loculicidal dehiscence. *H*, capsule of poppy (*Papaver*) poricidal dehiscence.

the **indehiscent** fruits. Examples of dehiscent fruits are: the poppy, lily, milkweed, pea, and bean. The fruits of sunflower, wheat, corn, rice, barley, oats, maple, carrot, celery, hazelnut, and many others are indehiscent fruits.

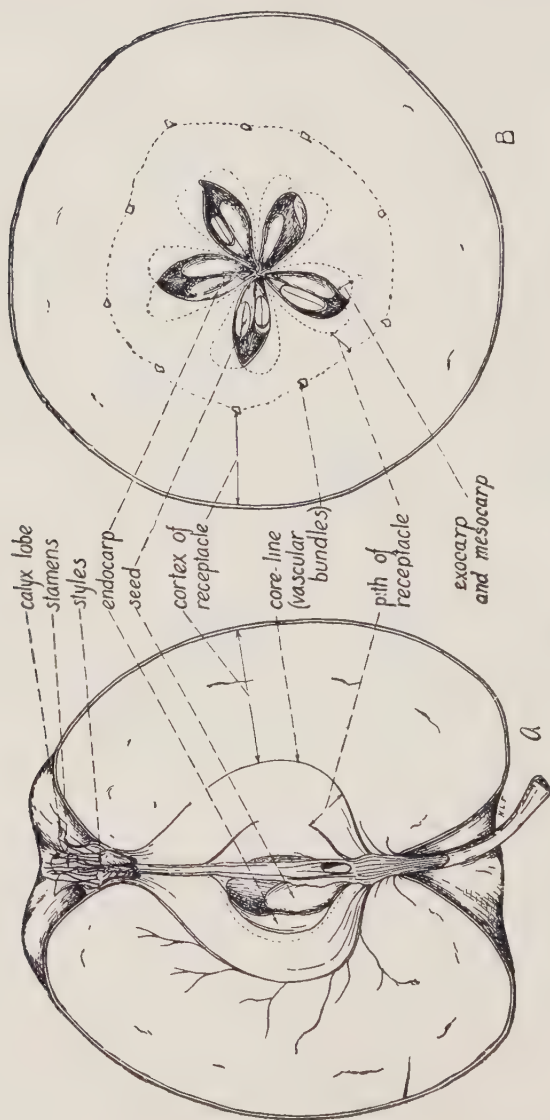


FIG. 112.—The mature apple fruit (pome). A, median longitudinal section. B, cross section.
(After Robbins, from *Botany of Crop Plants*.)

Aggregate and Multiple Fruits.—An aggregate fruit is one composed of a single receptacle upon which are massed many similar true fruits, and it is derived from a single flower having many pistils. The strawberry, raspberry, and blackberry are aggregate fruits.

Whereas an aggregate fruit is derived from a single flower having many pistils, a multiple fruit is developed from the ovaries of many separate and yet closely



FIG. 113.—Acorn of oak (*Quercus*), a nut.

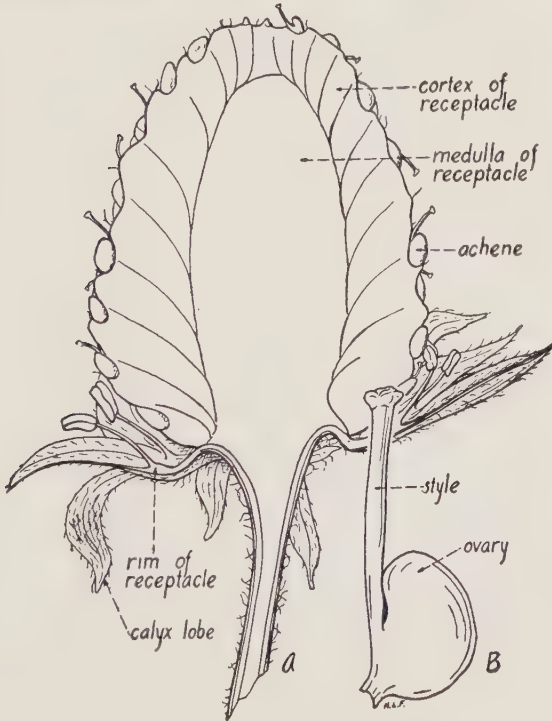


FIG. 114.—The aggregate “fruit” of strawberry (*Fragaria*). *A*, the “fruit” in median lengthwise section; *B*, single achene. (After Robbins, from *Botany of Crop Plants*.)

clustered flowers. Among the most familiar examples of plants bearing multiple fruits are the mulberry, pineapple, and fig.

THE SEED

Seeds are useful to man in a great many ways. He uses them as a means of multiplying useful plants. Seeds also furnish him with a large proportion of his food. The seeds of wheat and rice are the principal items of diet for a great part of the world's population. Second in importance to these great, staple foods are the other cereals, such as corn, rye, and barley, and the seeds of various beans. Many products used in the industries are also secured from seeds. Perhaps the most important of these are the various oils and fats produced from the seeds of such plants as the cocoanut (*Cocos nucifera*), cotton (*Gossypium*), flax (*Linum*), castor-oil plant (*Ricinus communis*), and peanut (*Arachis hypogoea*). These oils are used in the manufacture of soap, of substitutes for butter and lard, and as salad oil. Linseed oil is used in making paints, varnishes, artificial leather, oil-cloth, and linoleum. The vegetable ivory of commerce, from which great numbers of buttons are made, is secured from the seed of the South American palm (*Phytelephas*). Many other kinds of seeds furnishing important commercial products might be mentioned.

THE DEVELOPMENT OF THE SEED

Following fertilization, the ovule begins to undergo the changes which result in seed formation. Every seed consists of at least two parts, (1) the embryo and (2) the seed coat or seed coats. A third part called the endosperm is frequently present. It is enclosed, together with the embryo, within the seed coats. The embryo develops from the zygote, a single protoplast which is formed by the union of the egg cell of the embryo sac with one of the sperm nuclei of the pollen tube. The endosperm develops from the cell which is the result of the union of the polar nuclei

of the embryo sac with the second sperm nucleus of the pollen tube. The integuments of the ovule become the seed coats.

As the embryo and endosperm develop, they do so at the expense of the nucellus. Part of the nucellar tissue is digested and supplies food for the developing embryo and endosperm. As a result, the nucellus in the mature seed is usually represented by a thin layer of cells, generally much compressed, just within the seed coats.

In the following outline there are shown the structures into which the various flower parts develop as the fruit and seed are formed.

Flower		Mature Fruit and Seed	
Calyx.....		Adherent or deciduous	
Corolla.....		Usually deciduous	
Stamens.....		Usually deciduous	
Pistil {	Ovary {	Stigma.....	Withers; remnant may be present
		Style.....	Withers; remnant may be present
		Ovary wall.....	Pericarp { Exocarp Mesocarp Endocarp
		Placenta.....	Variously modified
		Ovule (seed) {	Funiculus..Seed stalk
			Raphe....Raphe
			Micropyle..Micropyle
			Nucellus...Perisperm (seldom present) or a thin layer of compressed cells
		Embryo sac {	Egg nucleus (fertilized) . . Embryo
			Polar nuclei (fertilized).. Endosperm

THE STRUCTURE OF THE SEED

Seeds of different plants vary greatly as to size, form, external color and markings, internal structure, and amount and nature of stored food, but most seeds consist of the following parts:

Seed coat or coats.

Remains of nucellus.

Endosperm—sometimes lacking.

Embryo	{	Plumule.
		Cotyledons (sometimes only one).
		Hypocotyl.
		Radicle.

The Seed Coats.—The seed coats are developed from the integument or integuments of the ovule. When two seed coats are present the inner one, the **tegmen**, is usually thin and delicate, while the outer one, the **testa**, is thick and tough, being a very effective protective structure. The principal external features of mature seeds are the **hilum**, **raphe**, and **micropyle**. The hilum is a scar which is always present but is often small and indistinct; it marks the place where the seed broke from the stalk (**funiculus**). In those plants in which the ovules become curved in development, so that the micropyle lies close to the hilum, there may be a ridge composed chiefly of a bundle of vascular elements. This ridge is called the raphe.

The Endosperm.—In seeds which when mature are without endosperm, the endosperm has been entirely consumed by the developing embryo before the seed became fully developed. In seeds of this type, such as the common bean, pea, alfalfa, and clover, the stored food is in the embryo itself, mostly in the cotyledons. Conspicuous examples of seeds with endosperm are castor-oil seed, corn, wheat, and other cereals.

The Embryo.—The rudimentary plant or embryo differs very greatly in appearance in different seeds, due generally to differences in the form and relative development of the parts of the embryo, for with few exceptions all embryos are made up of the same organs, which are:

1. The plumule—the terminal bud of the miniature plant (embryo). From this bud develops the shoot of the mature plant.
2. The cotyledon—(or cotyledons)—seed leaves.

3. The hypocotyl—portion from the attachment of the cotyledons to the upper end of the rudimentary root.

4. The radicle—rudimentary root.

The plumule, hypocotyl, and radicle together form the axis of the embryo. At germination the plumule develops into the shoot and the radicle gives rise to the primary root. The cotyledons are temporary leaves attached laterally to the axis of the embryo and are unlike typical foliage leaves because of their adaptation to the function of food storage or of food absorption

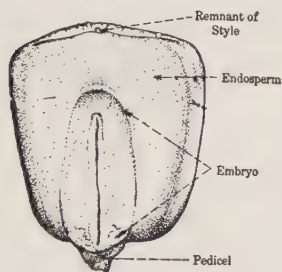


FIG. 115.—Fruit (grain) of corn (*Zea mays*), external view. The small projection at the upper end of the grain is the base of the style (strand of corn silk).

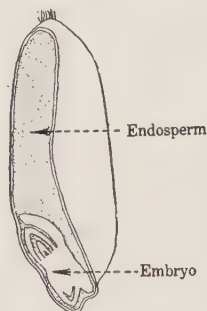


FIG. 116.—Longitudinal section of wheat grain showing the endosperm and embryo of the seed.

from the endosperm. In some cases they may carry on photosynthesis for a time. The portion of the main axis of the embryo below the cotyledon and above the radicle is called the hypocotyl. It is often difficult to determine, without studying cross sections of the embryo microscopically, just where the radicle and the hypocotyl join. In the case of many species it is in the hypocotyl that the transition takes place from the arrangement of phloem and xylem which is characteristic of the stem to that found in young roots, that is, from the arrangement in the stem in which the phloem lies outside of the xylem to the alternating radial arrangement characteristic of young roots. At the extreme tip of the radicle there is a growing point provided with a root cap,

such as is found in all typical roots. Sometimes the plumule consists merely of the stem growing point, but in many seeds the growing point of the plumule has already given rise to a number of rudimentary foliage leaves, which surround it, as in the terminal buds of mature plants.

KINDS OF FOOD STORED IN SEEDS

The principal kinds of food stored in seeds are as follows:

1. Carbohydrates, chiefly
 - (a) Starch,
 - (b) Hemi-celluloses,
 - (c) Sugars.
2. Fats.
3. Proteins.

Starch.—This is the commonest form of food stored in seeds. It may occur either in the embryo or in the endosperm. It is formed in the cells of the developing seed by the leucoplasts from the sugar which is conducted to the seeds from other parts of the plant. The form of the starch grains produced by the leucoplasts varies in different plants, and the characteristic forms and markings of the grains (see Fig. 117) are valuable aids in the recognition of certain adulterations in foods.

Hemi-celluloses.—The hemi-celluloses are complex reserve carbohydrates. They constitute the greater part of the thickened cell walls of the endosperm in the seeds of such plants as the date (*Phoenix dactylifera*), onion (*Allium*), coffee (*Coffea*), and vegetable ivory palm (*Phytelephas monocarpa*). Hemi-celluloses are quite different from true cellulose, and since they are more easily rendered soluble (digested) are more available as reserve food for the developing embryo at germination.

Fats.—Fats are of general occurrence in both vegetative and reproductive organs of plants, but are much more abundant in

seeds than elsewhere, and constitute an important reserve food. Fats occur in the form of globules within the protoplasts of the cells, usually being much more abundant in the embryo than in the endosperm.

Proteins.—The proteins are organic compounds containing oxygen, hydrogen, carbon, nitrogen, generally sulphur, and often phosphorus. Next to water, proteins are the most abundant constituents of protoplasm, and are essential for the production of new protoplasm. Stored proteins are found in all seeds, occurring very abundantly in seeds of members of the bean family (*Leguminosae*).



FIG. 117.—Starch grains from different sources. 1, *Diffenbackia* (After Meyer); 2, *Triticum sativum*; 3, *Phaseolus lunatus*; 4, *Phaius*; 5, *Canna*; 6, *Solanum tuberosum*; 7, *Zea mays* (1–7, after Reichert.)

DESCRIPTION OF REPRESENTATIVE TYPES OF SEEDS

Common Bean.—*Dicotyledonous Seed without Endosperm.*—(Fig. 118.) A large oval scar called the hilum, near the middle of one edge of the seed, marks the place where the seed broke from the stalk or funiculus in the fruit (pod). At one end of the hilum is a small opening, the micropyle, which was present in the ovule at the time of fertilization. The micropyle is more easily seen if the seed

is soaked in water. The position of the radicle is indicated by an elevation of that part of the seed coat which is adjacent to the micropyle. The seed coats of the bean may be easily removed from seeds which have been soaked in water. When the seed coats have been removed, the embryo of the seed is visible. This embryo consists of the following parts: (1) two cotyledons or

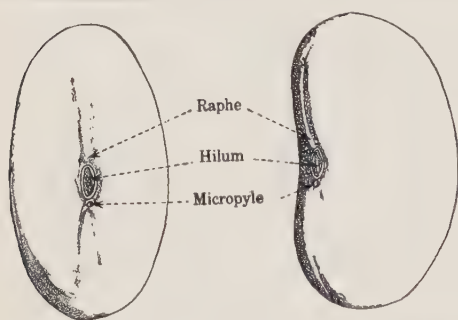


FIG. 118.—Two views of a seed of a common bean (*Phaseolus vulgaris*).

seed leaves, between which is the (2) plumule with two minute foilage leaves, enclosing the growing point, and (3) the hypocotyl, terminating in the (4) rudimentary root or radicle. The two cotyledons are large and fleshy and contain stored food, chiefly starch. Although

the leaves are small, the veins within them can be easily seen.

The endosperm is lacking in the mature bean seed, having been absorbed by the developing embryo. In seeds of this type the cotyledons are the storage organs.

Castor-oil Seed.—*Dicotyledonous Seed with Endosperm.*—At one end of the castor-oil seed is a spongy structure, the caruncle, which is an outgrowth of the testa. It covers and obscures the micropyle. Adjacent to the caruncle is the hilum, and running approximately the full length of the seed is the raphe. Sections of the seed show the embryo embedded in a massive endosperm.

The embryo of the castor-oil seed consists of two flat cotyledons, a very short hypocotyl, a diminutive plumule, and a short radicle. The relatively slight development of the plumule and radicle in the castor-oil seed is characteristic of many dicoty-

ledonous seeds having endosperm. In dicotyledonous seeds in which the endosperm is used up by the embryo before the seed

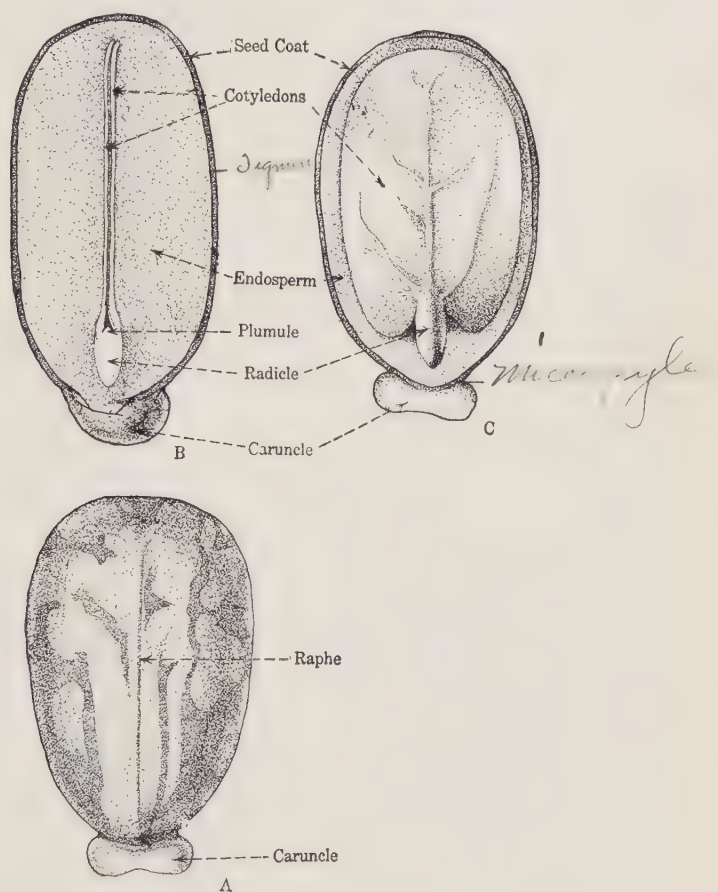


FIG. 119.—The seed of castor-oil plant (*Ricinus communis*). A, external view. B, median longitudinal section cut at right angles to the broad surface of the cotyledons. C, median longitudinal section, cut parallel with the broad surface of the cotyledons.

ripens (as in the bean) the plumule and radicle are generally larger and more differentiated.

Wheat Seed.—*Monocotyledonous Seed with Endosperm.*—In the mature fruit there is a tuft of hairs, the **brush**, at the small (stigmatic) end of the grain. The embryo lies at the base of the grain, the rest of the contents being endosperm.

The structure of the embryo of the wheat grain is shown in a drawing of a median longitudinal section. The radicle is surrounded by the root sheath or **coleorhiza**. Between the radicle and the point of attachment of the cotyledon is the very short hypocotyl. The stem growing point and foliage leaves (together forming the plumule) are surrounded by a leaf sheath, the **coleoptile**.

In wheat, as in all members of the grass family, there is a single cotyledon. It is a structure which lies in contact with the endosperm and is specialized to absorb food (starches and proteins) from the endosperm and turn it over to the growing parts of the embryo; accordingly, the cotyledon remains within the seed during germination. This cotyledon, which never develops into a green leaf-like structure, in contrast to the cotyledons of the castor-oil seed and some beans, is called the **scutellum**. On the opposite side of the hypocotyl from the scutellum is a small projection which, it has been suggested, represents a suppressed second cotyledon.

DISSEMINATION OF SEEDS AND FRUITS

The migration of plants over the surface of the earth is accomplished in many different ways. We have seen that some plants migrate by means of runners, or rhizomes; this method is very slow. In others, such as the tumbleweeds, the whole plant is carried by the wind, rolling for many miles over treeless areas, scattering seeds as it travels. But the most effective and rapid means of plant migration is by means of seeds or fruits.

There are many structural modifications by which dissemination of seeds and fruits is secured (see Fig. 120). **Wind, water, and animals**, including man, are the chief agencies in seed and

fruit dissemination. Fruits and seeds which are winged (example, maple) or have long silky hairs (cotton, milkweed), or tufts of hairs (dandelion) are readily carried by wind. Some fruits

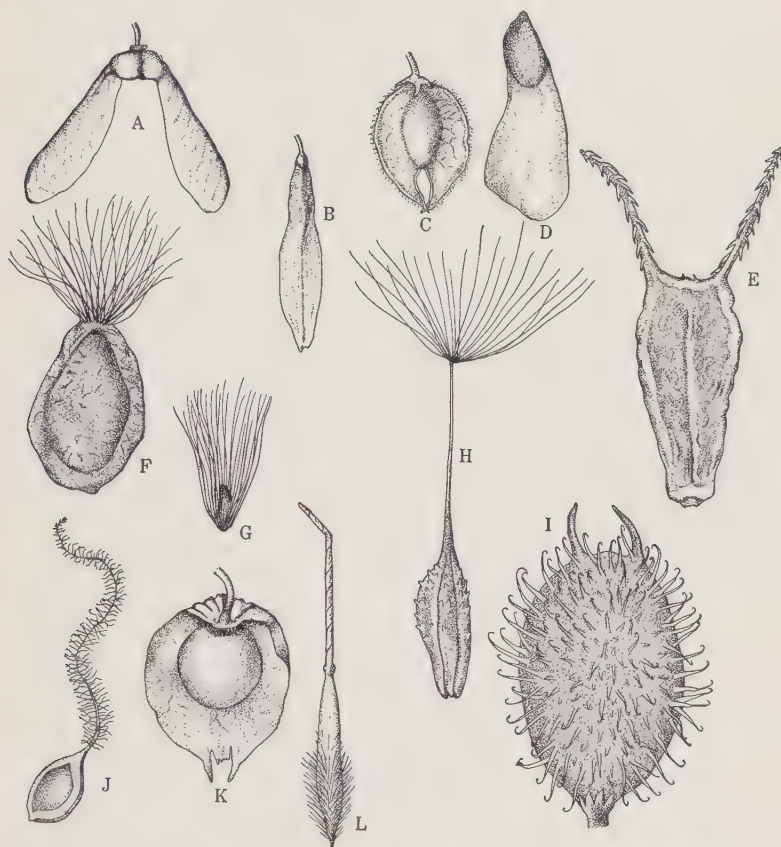


FIG. 120.—Various seeds and fruits showing special provisions for dissemination. *A*, winged fruit of maple (*Acer*). *B*, winged fruit of ash (*Fraxinus*). *C*, winged fruit of elm (*Ulmus*). *D*, winged seed of pine (*Pinus*). *E*, barbed seed of Spanish needles (*Bidens*). *F*, milkweed (*Asclepias*) seed with tuft of hair. *G*, hairy seed of cottonwood (*Populus*). *H*, fruit of dandelion (*Taraxacum*) with parachute-like tuft of hairs. *I*, hooked fruit of cockle-bur (*Xanthium*). *J*, fruit of *Clematis* with long, plume-like style. *K*, fruit of ground cherry (*Physalis*), with membranous envelope. *L*, bearded fruit of porcupine grass (*Stipa*).

have membranous envelopes containing air and are carried easily by wind or water. Many seeds will float though lacking special adaptations which insure buoyancy. Numerous fruits and seeds have hooks, barbs, beards, and spines which adhere to the hair of animals or to the clothing of man. The seeds of fleshly edible fruits are scattered by birds and animals, nuts are carried away and hidden by squirrels, and weed seeds may be

transported to distant parts of the earth as "impurities" in shipments of commercial seed.



FIG. 121.—The squirting cucumber, *Echinosiphon elaterium*, one of a number of different kinds of "explosive" fruits in which seed dissemination results from violent rupture of the fruit. (From Bocquillon.)

A seed is essentially a young plant (embryo) arrested in its development. An individual plant does not start its life as a seed. It will be recalled that instead it starts its life as a single cell called a zygote. The new individual plant comes into existence at the time of fertilization—when a sperm (male) nucleus from the pollen tube fuses with the egg (female) cell in the embryo sac of the ovule,

forming a zygote. This single protoplast produced by the fusion of two protoplasts undergoes repeated division, and by growth and differentiation there results a young plant which, with its surrounding protecting coats and its stored food, is called the seed. After the seed has matured there is normally a period during which growth and development of the embryo are at a standstill. Resumption of these activities is called germination.

Conditions Necessary for Germination.—For this resumption of growth and development the following external conditions

are essential: (1) a sufficient supply of water, (2) a favorable temperature, and (3) a supply of oxygen. If any one of these is lacking the seed will not germinate.

Water.—Water plays a most important rôle in the germination of seeds.

1. Water softens the seed coats, and thus enables the embryo to break through them more easily.

2. The water absorbed by embryo and endosperm causes the seed to swell and this results in the bursting of the seed coats.

3. Water facilitates the entrance of oxygen into the seed. Dry cell walls are almost impermeable to gases, but if the walls have imbibed considerable water, gases can diffuse quite readily through them. As the walls of the cells of the seed coats and embryo take up water an increased oxygen supply to the living cells results and more active respiration is made possible. On the same account the carbon dioxide produced by respiration is able to diffuse outward.

4. Water dilutes the protoplasm and permits its various normal functions, including digestion, respiration, and assimilation, to go on actively. Since the protoplasm of the cells of the embryo and other living parts of the seed loses most of its water before the seeds are shed, its activities are almost completely suspended from that time until germination.

5. Water makes possible the transfer of soluble food from the endosperm or cotyledons to the growing points of the embryo, where food is necessary for the building up of new protoplasm.

Favorable Temperature.—For the seeds of any kind of plant there is a temperature, called the **minimum temperature**, below which germination will not take place. There is also a **maximum temperature** above which the seeds will not germinate and an **optimum temperature** at which germination goes on most rapidly. These cardinal temperatures vary widely in different species.

Oxygen.—Oxygen is essential for germination, because without it respiration can not go on in the seed. Respiration is very active in germinating seeds, as it is in all tissues where growth

and other cell activities are proceeding at a high rate. On that account large quantities of oxygen must be available to the seed if germination is to proceed normally.

THE GERMINATION PROCESS

The principal processes going on in the seed during germination are:

1. Absorption of water by imbibition and osmosis.
2. Digestion.
3. Food transfer.
4. Assimilation.
5. Respiration.
6. Growth.

Water Absorption.—The initial process in seed germination is the absorption of water. The functions of the absorbed water have already been mentioned.

Digestion.—In the seed the stored foods can not be transported from cell to cell and utilized in building up protoplasm and cell walls until they are changed into a soluble and hence diffusible form. The process of rendering foods soluble and diffusible is termed digestion. In this process certain digestive agents, which belong to the class of substances called **enzymes**, are required.

Enzymes are substances, probably protein in nature, which are produced in living cells of plants and animals and resemble inorganic catalysts, such as platinum, in that certain chemical changes go on very rapidly in their presence but very slowly or scarcely at all when they are not present. They greatly accelerate the rate of many important changes in cells which otherwise would practically not go on at all. Also, due to the presence of the proper enzymes, changes may go on in living cells at relatively low temperatures (below 40° Centigrade) which would otherwise go on at the same rate only at such high temperatures as would

be fatal to all living protoplasm. No enzyme has been secured in sufficient purity to determine its exact composition. The principal characteristics of enzymes may be summarized as follows:

1. They are produced by living protoplasm.
2. They may be separated from protoplasm and still retain their activity for years if stored under proper conditions.
3. They are effective in small quantities.
4. They are sensitive to heat; heating to 60° C. permanently renders them ineffective.
5. They are generally specific, one enzyme being effective in one chemical change only. Thus diastase changes starch to certain sugars and zymase converts glucose into alcohol and carbon dioxide, but neither is able to affect any chemical change other than the characteristic one mentioned.

Digestion, rendering insoluble substances soluble and diffusible, is only one of many different kinds of changes which are brought about by enzymes.

The principal classes of digestive enzymes found in seeds and the products of the digestion which they carry on are:

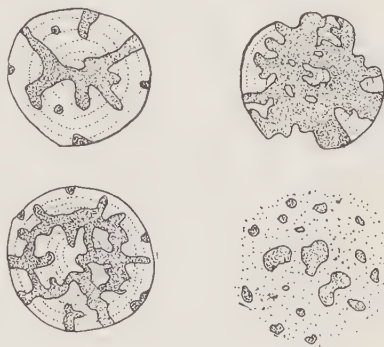


FIG. 122.— Digestion of starch grains by diastase. The four figures show successive stages of digestion. (Redrawn from Strasburger.)

Enzyme	Substances Digested	Soluble Products
Amylase (diastase)	starch	maltose (a sugar)
Cytase	hemi-celluloses	mannose and galactose (sugars)
Lipase	fats	glycerine and fatty acids
Proteases	proteins	amino acids

Food Transfer.—Absorption of water, the secretion of enzymes, and digestion are but preliminary to the transfer of food from the storage cells to the growing parts of the germinating seed. Conductive tissue is poorly developed in the rudimentary plant or embryo seed, hence transfer of material from one part to another must be almost entirely by diffusion from one living cell to another. From our discussion of diffusion in Chapter II we learned that any substance tends to diffuse from a region where there are more dissolved particles of that substance per unit volume of solution to a region where there are fewer particles of that same substance per unit volume. At the growing points of the embryo soluble foods are being transformed into cellulose walls and into protoplasm, and are thus being removed from solution. Hence a constant reduction in the concentration of soluble foods is going on at the growing points. The direction of movement of soluble foods is toward these points of relatively low concentration of such substances, and away from the parts of the seed (storage regions) where soluble foods are being produced by the action of enzymes upon the insoluble stored food.

Assimilation.—This is the final step in the utilization of the stored food. It is the transformation of the digested foods into the living substance, protoplasm, and of certain of these foods by the protoplasm into cell walls. The change from dead to living matter may be said to be the most important and most interesting which takes place in organisms. We know almost nothing about the process, however, for an understanding of it would necessitate our first learning much more than is now known of the actual nature of protoplasm.

Respiration.—Respiration goes on more actively in germinating seeds than in almost any organ or tissue of green plants. It will be recalled that respiration is an energy-releasing process in which part of the food is broken down into very much simpler compounds, such as carbon dioxide and water (see Fig. 123), and the energy stored in the food is released. This released energy is in part used by the seedling plant in the work of build-

ing up the complex compounds of which the plant is composed. Much of it, however, is dissipated as heat.

Growth.—The swelling of the seed, due to imbibition of water and to growth, is followed by the bursting of the seed coats. This rupture may be caused by the radicle, as in many dicotyledonous plants, or by the cotyledon, as in many monocotyledons. Freed

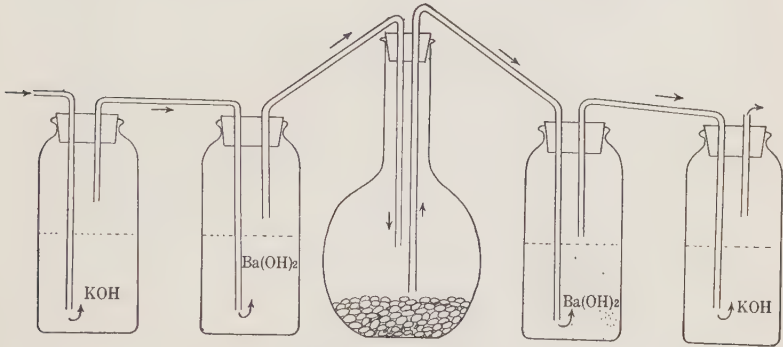


FIG. 123.—Diagram of apparatus used to demonstrate the evolution of carbon dioxide from respiring seeds. Air enters the apparatus by the tube at the left and passes through in the direction shown by the arrows. As the air bubbles through the solution of potassium hydroxide (KOH) in the first bottle the carbon dioxide gas in the air is absorbed by the solution, potassium carbonate being formed and remaining in the solution. The air next passes through a solution of barium hydroxide $\text{Ba}(\text{OH})_2$ to show whether all the carbon dioxide has been absorbed by the KOH solution. If the carbon dioxide had not been completely removed a white precipitate of barium carbonate would be formed. The absence of any such precipitate shows that the air passing into the flask containing the germinating seeds is free of carbon dioxide. The evolution of carbon dioxide by the seeds in the flask is shown by the formation of the white precipitate of barium carbonate (BaCO_3) as the air from the flask is drawn through the next bottle. The KOH bottle at the right serves to prevent any carbon dioxide from passing in the reverse direction.

from the seed coats, supplied with water and dissolved foods and with oxygen for respiration the embryo now grows actively. Its growth is due (1) to the enlargement of cells in the embryo, which are already formed, and (2) to the production of new cells at the growing point of the radicle and the

plumule. The radicle is usually the first embryo structure to protrude from the seed. It grows downward, sends out branches, develops root hairs, and thus increases its absorbing surface.



FIG. 124.—Stages in the germination of wheat. *c*, coleorhiza; *g*, coleoptile; *r*, roots; *s*, embryo. (After Bocquillon.)

In many plants, such as the common bean, sunflower, and squash, the cotyledons and plumule are brought up to the light by the growth of the hypocotyl, and the seed coats generally remain in the soil. In oaks and in other plants, such as garden pea and scarlet runner bean, the cotyledons remain below the ground. In the cereals the one cotyledon (scutellum) does not even emerge from the seed. After the young plant reaches the light and develops

chlorophyll-bearing tissue, it is no longer completely dependent upon the store of reserve food within the seed, but is now able to carry on photosynthesis.

CONDITIONS AFFECTING THE VITALITY OF SEEDS

Many factors affect the vitality of seeds, that is, the capacity to germinate and produce seedlings capable of developing into adult plants. Weakly parent plants often produce seeds which grow into plants of less vigor than those resulting from normal seeds. Most seeds require dry atmospheric conditions in order to mature properly. Seedlings are usually most vigorous when grown from seeds which have been allowed to reach full maturity on the plant. All seeds gradually lose their vitality with the lapse of time, although a few cases are known where germination has occurred after a period of 150 or 200 years. Care should be taken as to the manner of storing mature seeds, low temperatures and dryness being desirable to prevent germination during storage and to retain the vitality of the embryos.

DORMANCY OF SEEDS

Many seeds are incapable of germination immediately after they mature. This characteristic is known as **dormancy** or **delayed germination**, and the causes vary in different types of seeds. Some seeds have embryos which are rudimentary at ripening time, and their development must be completed before germination is possible. In other cases the tissues surrounding the embryo retard gaseous exchange, or water intake may not occur due to the high impermeability of the seed coats to that liquid. Sometimes the embryo is incapable of rupturing the seed coats and this must be accomplished by outside agencies, such as the action of soil organisms, and freezing and thawing. Another process known as **after-ripening**, which is sometimes associated with increase in acidity of the cell sap, appears to be a necessary preliminary to germination in some seeds.

SEEDLINGS

From the time when the young plant emerges from the seed coats to the time when it becomes entirely dependent upon food manufactured by itself it is called a seedling. Seedlings may be divided into two quite distinct types:

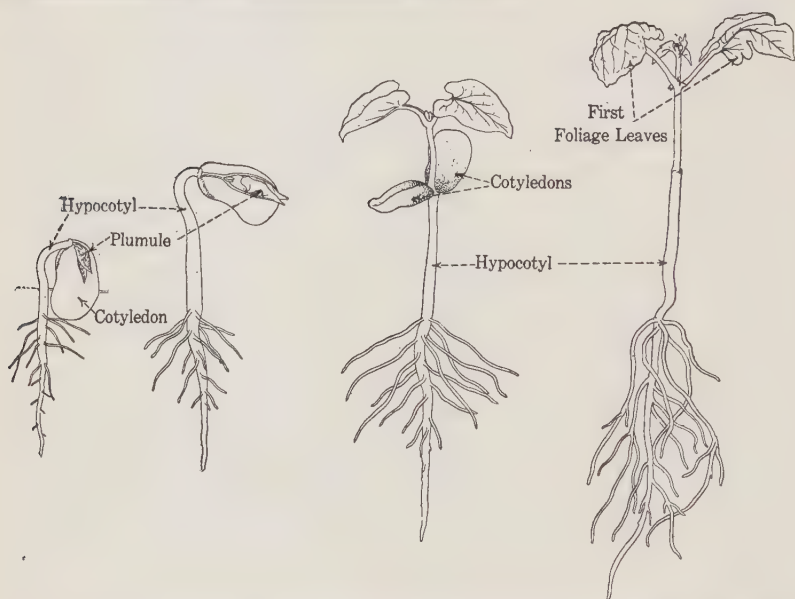


FIG. 125.—Successive stages in the germination of the seed of the bean (*Phaseolus vulgaris*).

1. In the first of these types the cotyledon or cotyledons are raised above the ground by the lengthening of the hypocotyl. Some of the stored food in the cotyledons is used by the developing root, but a considerable quantity remains, and before this is exhausted, the cotyledons, which are now in the light, become green and carry on photosynthesis to some extent. As the foliage leaves formed by the plumule gradually develop and take on their functions, the remainder of the reserve food is used up, and

the cotyledons shrivel. A familiar example of this type of seedling is the common bean (*Phaseolus vulgaris*).

2. In the second type the cotyledon or cotyledons remain beneath the ground. In this type of seedling the hypocotyl undergoes little or no elongation. This type is illustrated by

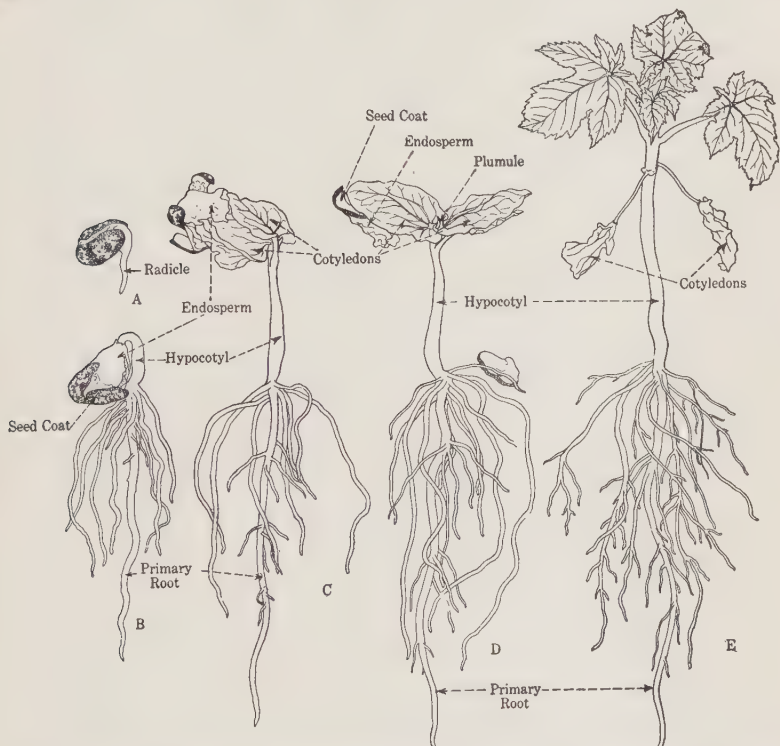


FIG. 126.—Successive stages in the germination of a seed of castor-oil plant (*Ricinus communis*).

wheat and all other grasses. The cotyledons remain within the seed coats and in species lacking endosperm serve as a food-storing organ only. In seeds with endosperm the cotyledons act as food-absorbing organs for the embryo and may or may not serve temporarily as photosynthetic organs also.

CHAPTER VIII

RELATION OF THE PLANT TO ENVIRONMENT

THERE are various external conditions or factors which influence the development, structure, and activities of the various organs of the plant. Collectively, these external factors are spoken of as the **environment**. It is convenient to classify the environmental factors into three groups:

1. **Climatic factors**, those which act upon the plant through the atmosphere.
2. **Edaphic factors**, those which operate through the soil.
3. **Biotic factors**, those arising from the presence of other plants and animals.

Some of the principal factors under each of these three groups are:

Climatic factors—

Temperature
Illumination
Carbon dioxide concentration
Atmospheric humidity and precipitation
Wind

Edaphic factors—

Available water in the soil
Air in the soil
Temperature of the soil
Quantity and nature of the soil solutes

Biotic factors—

- Competition among different species
- Grazing by animals
- Soil bacteria, algae, and protozoa
- Parasitic fungi
- Insects that injure plants
- Insects that carry on pollination

TEMPERATURE

Each of the physiological processes which go on during the life of the plant has certain temperature limits (maximum and minimum) between which it can take place, and a characteristic optimum temperature at which it goes on most actively.

The minimum, optimum, and maximum temperatures for one process may differ considerably from those of another process taking place in the same plant at the same time. Moreover, in the case of a given process, such as photosynthesis, these temperatures may vary rather widely in different species. The minima seldom are lower than one or two degrees above 0°C. , and the maxima are generally below 45° .

Injury resulting from freezing temperature appears to be due, in part at least, to the rapid withdrawal of water from the cells; this is accompanied by the formation of ice crystals in the intercellular spaces.

In some cases the resistance to low temperatures seems to be concerned with as yet unexplained peculiarities of the protoplasm, which make it immune to the injurious effects attending ice formation. In other cases it is undoubtedly due to certain substances, as sugar, which are present in the cell sap in such quantities as to prevent freezing of the water in the protoplasm except at very low temperatures. Plant parts whose protoplasm is relatively low in water content (seeds, for example) can withstand very low temperatures without injury. Often young shoots whose living tissues contain much water are killed by frost though older stems whose cell sap is more concentrated may

survive. The maturing of plant tissues that takes place in late summer, autumn, or early winter seems to influence the resistance to winter temperatures. Well-matured tissues are more resistant than those not completely matured.

Gardeners commonly practice the process of "hardening" their transplants. If a tomato plant, for instance, is removed suddenly from a warm greenhouse in the spring to the garden out of doors, it has little resistance to low temperatures, and the death point (temperature at which it will be killed by cold) is relatively high. The usual procedure is to move the plants from the greenhouse to a cold frame where, after remaining for a time where the temperatures are intermediate between those of the greenhouse and out of doors, the plants may be planted with safety in the open.

Differences in temperature in different parts of the world and at different altitudes constitute what is probably the most important factor in determining what plants shall or shall not grow in a given region.

ILLUMINATION

By the term light we mean to include all the energy (radiant energy) which reaches the plant from the sun. Light may affect the plant and its activities in the following ways:

1. By reason of the dependence of the process of photosynthesis on the intensity of illumination.
2. By heating of tissue due to the absorption of radiant energy especially of longer wave length.
3. By furthering transpiration through heating of the leaf.
4. By its effect upon the orientation of leaves and other organs. The leaves of shade plants are almost always more or less horizontal so that light falls upon them at right angles to their surface. The leaves of some sun plants hang down or are held perpendicular so that the sun's rays most of the time strike the leaf surface at an acute angle. Thus much less radiant energy is absorbed by the leaves.
5. By its effect upon distribution of plants over the earth's surface.

6. Not only by the effect of light intensity but of duration of illumination upon the rate of growth and development of plants and particularly upon flower production. There is evidence in the case of certain crop plants that the development of flowers is dependent not so much upon the intensity of light as upon the relative length of day and night. Some plants which flower only during the long days of June can be made to bloom in mid-winter, if the length of daily illumination is increased by means of electric lights. Other plants which normally bloom and fruit in the autumn when the days are short, can be made to bloom and fruit in mid-summer, if the length of day is shortened by placing them in the dark a part of each day.

7. By its effect upon the form of the shoot system. The difference between the form of trees which have developed as isolated individuals and that of others of the same species which have grown in a forest, closely surrounded and accordingly largely shaded by other trees, is due to differences in illumination.

8. By its effect upon the form and internal structure of leaves. The following are the principal anatomical characteristics of the leaves of sun plants and shade plants.

SUN PLANTS

Thick palisade parenchyma, due to increase in length of cells or in number of layers of cells.

Spongy parenchyma not well developed.

Thick leaves.

Small intercellular spaces.

Thick and heavily cutinized epidermis.

Stomata confined to lower side or more abundant on the lower side.

Frequently smooth and shiny surface, capable of reflecting much of the light falling upon them.

Often densely hairy.

SHADE PLANTS

Thin layer of palisade cells or none at all.

Well-developed spongy parenchyma.

Thin leaves.

Large intercellular spaces.

Thin and slightly cutinized epidermis.

Stomata on both sides, the number on the two sides nearly or quite the same.

Generally dull surfaces.

Seldom very hairy.

Similar differences are frequently found between different individuals of the same species which are growing respectively in sunny and in shaded habitats.

CARBON DIOXIDE

Under natural conditions the concentration of carbon dioxide in the atmosphere is very low (3 parts in 10,000) and varies only within narrow limits. Accordingly, though this factor in the environment is of immense importance, there are no recognizable effects upon plants growing naturally which can be attributed to differences in carbon dioxide supply.

PRECIPITATION AND ATMOSPHERIC HUMIDITY

Precipitation.—The significance of water for the life of the plant and the indispensable rôles which it plays in the various vital processes have already been discussed (Chapter IV, pages 93 and 94). Precipitation is a factor second in importance only to temperature in determining the distribution of different plants in the various regions of the earth. It is not so much the total amount of rain falling throughout the year as the distribution of the rain over the whole year which determines what kind of plants will grow in a given region. For example, in the tropics where the rainfall is heavy and rather uniformly distributed throughout the year, the dominant vegetation is an evergreen forest; on the other hand, in those parts of the tropics where the total rainfall for the year is equally heavy, but occurs during a few months of the year, the forests are chiefly of the deciduous type.

Atmospheric Humidity.—Even in the driest regions there is always some water present in the air in the form of gas (water vapor). The water vapor in the atmosphere is spoken of as atmospheric humidity. When the air contains all the water vapor it can hold it is said to be saturated, but the percentage of water in a saturated atmosphere varies widely with the tem-

perature. Air which is saturated when it is at a low temperature will be far from saturated at a considerably higher temperature, for with rise in temperature its capacity for holding water vapor increases. Air saturated at a relatively high temperature loses some of its water vapor when it is cooled. When that occurs small drops (mist or fog) or larger drops (rain) are formed but the air remains saturated at the lower temperature. Any subsequent increase in temperature results, however, in the air becoming less than saturated, unless it absorbs water meanwhile from free water surfaces. The humidity of the air surrounding the plant is the most important single factor in determining the rate of transpiration. Low humidity is often assumed to be principally responsible for the various devices which plants employ to reduce transpiration. (See discussion of transpiration, Chapter V, pages 126 to 129.) It is not, however, the percentage of water vapor in the atmosphere which determines, other things being equal, how rapid transpiration shall be. It is, instead, the percentage of water which the air can still absorb before saturation is reached. With a given percentage of water in the atmosphere, this quantity increases with increase in temperature.

WIND

One of the principal, although indirect, effects of wind on plants is that of increasing the rate of transpiration. Aside from the indirect effects of wind upon the plant, there are various direct effects. Thus in locations where there are strong prevailing winds the trees are generally smaller than in other localities, the trunks are frequently bent away from the wind, and branches on the windward side are often almost entirely suppressed so that the tree has a one-sided form. Certainly the deformations of the exposed trees on sea coasts and on mountain tops are largely due to strong winds, though in the latter case the weight of the winter snow accumulated on the branches is also an important factor.

AVAILABLE WATER IN THE SOIL

By far the most important of the environmental factors which have to do with the soil (edaphic factors) is the supply of soil water available to the roots of plants. We shall enumerate the principal factors determining the quantity of available water and mention some of the effects upon the plant of differences in the quantity.

Principal Factors Influencing the Available Water in the Soil.—

1. The amount of annual precipitation.
2. The distribution of precipitation over the year.
3. The humidity of the atmosphere, since it affects the rate of water loss from the soil by evaporation.
4. The distance of the water table (level of standing water in the soil) below the surface of the soil. The fluctuations in this from one season to another depend chiefly upon the precipitation and evaporation.
5. Rate at which water percolates downward into the soil. This is most rapid in sandy soil, and progressively slower in clay and humus.
6. The power of the soil to raise water from lower levels (the water table) by capillarity. Water is raised much higher by capillarity in clay soil than in sandy soil, but it rises at a more rapid rate in sandy soils than in clay soils.
7. Vegetation. Plants growing in soil may greatly decrease the amount of water in the soil. On account of the water absorbed by the roots and lost by transpiration from other plant organs, the soil may lose water much more rapidly than if it were bare.

The importance of the available water in the soil is so great in its effect upon plants that botanists are accustomed to classify plants, as regards their relations to environment, on the basis of their water requirements. They recognize:

1. **Xerophytes.**—Plants which are very resistant to drought or live in very dry places: Russian thistle (*Salsola*), millet (*Setaria italica*), sorghum (*Andropogon*), cactus (*Opuntia* and other genera), sagebrush (*Artemisia tridentata*).

2. **Hydrophytes.**—Plants which live in water or in very wet soil: cat tail (*Typha*), water lilies (*Castalia*, *Nelumbo*), sedges (*Carex*).

3. **Mesophytes.**—Plants growing best with moderate water supply: the common plants of meadow and forest.

4. **Halophytes.**—Plants able to grow in salt marshes and alkali flats where there may be an abundance of water in the soil but where, on account of the high concentration of the soil solution, water is absorbed with difficulty: greasewood (*Sarcobatus*), salt brush (*Atriplex*), sugar beet (*Beta*), glasswort (*Salicornia*).

AIR IN THE SOIL

The quantity of air in the soil is of considerable importance to plants growing in it. The living cells of the root must have oxygen in order to respire. Respiration is particularly active in the cells of the growing points and the actively growing regions near them. Normally the roots secure the necessary oxygen for respiration by its diffusion into the roots through the root hairs and ordinary epidermal cells. A moderately dry soil, not excessively fine in texture, contains much air in its pores. A very wet soil contains less air than would the same soil in a drier condition, for part of the space (that of the larger interstices) which would be occupied by water in the wet soil is occupied by air in the drier soil. In a water-soaked soil there is practically no air save that which is dissolved in water. As a rule, the larger the soil particles and the looser and more porous the soil the better its aeration. Most plants die if the soil about their roots is continuously water-soaked. Their death is presumably due principally to insufficient oxygen supply. There are some plants, however, which can thrive although the root system is

submerged in water or surrounded by a soil which is water-soaked. Almost all such plants contain in the stem and root large communicating air spaces. Thus air absorbed into the leaves and stems may reach the living cells of the root in sufficient quantity. Some, like the bald cypress (*Taxodium distichum*) and various species in tropical mangrove swamps, produce special root branches which grow upward until their ends are above the water level. These special root branches have a central core of loose parenchymatous tissue through which air is said to pass downward to the submerged parts.

SOIL TEMPERATURE

The temperature of a soil may greatly influence the plants which grow in it. One of the principal effects of low soil temperature is the reduction of the rate of water absorption by the root. Plants whose roots are in a soil containing abundant water may wilt if the temperature is very low.

QUANTITY AND NATURE OF THE SOIL SOLUTES

Water absorption by the roots can take place only if the concentration of the cell sap of the root hairs is greater than that of the soil water. The adaptations of plants growing naturally in salt marshes or in so-called **alkali** soils resemble those of plants growing in very dry soils or in an atmosphere of very low humidity. If the root systems of most plants were exposed to such concentration as exists in salt, swampy, and strongly "alkali" soils, they would not be able to absorb sufficient water to replace that lost by transpiration and would soon die.

The soil water of some soils is deficient in one or more of those essential elements which the plant must secure from the soil. These elements, it will be recalled, are potassium, calcium, magnesium, iron, nitrogen, sulphur, and phosphorus. Plants growing

in such soils have their growth rate much reduced and remain dwarfed.

Most seed plants thrive best in a slightly acid soil, but there is a wide variation in the tolerance of different plants for acid and slightly alkaline soils. Certain plants, such as sour dock (*Rumex acetosella*) and heather (various *Erica* species), growing normally on quite acid soils, do not thrive in soils which are rich in lime. This is probably due to the fact that such soils are not sufficiently acid.

THE INFLUENCE OF CERTAIN BIOTIC FACTORS UPON PLANTS

Other species of organisms, both plants and animals, are as much a part of the environment of a given plant as are the various climatic and edaphic (soil) factors which we have mentioned, for in nature plants compete for space, light, water, and inorganic salts.

Grazing by wild or domestic animals may greatly affect the plants growing in a certain habitat. Most species are unable to survive the constant removal of leaves and parts of the stem by grazing animals. As a result, those plants (principally certain grasses) which are able to withstand cropping and to spread without seed formation tend to take full possession of a closely grazed piece of land.

The soil itself contains many simple organisms, such as algae, bacteria and other fungi, and protozoa. Some of these, particularly certain of the bacteria, raise the fertility of the soil by increasing the amount of nitrogen available for the seed plants growing in it. In the absence of certain of these organisms, plants belonging to the bean family (*Leguminosae*) remain stunted. Other organisms in the soil may be injurious to seed-bearing plants either because they lessen soil fertility (some of them greatly reduce the available nitrogen) or because they are the cause of root diseases.

Parasitic organisms, bacteria and other fungi, nematode worms, and insects are biotic factors of very great importance. The insect parasite, *Phylloxera*, which at one time destroyed most of the French vineyards, the fungus parasite causing chestnut blight, which has killed many of the chestnut trees of the United States, and the parasitic fungus responsible for the white pine blister rust, which has practically wiped out the white pines of the eastern United States, are particularly striking illustrations of the importance of parasitic plants and animals as living factors in the environment surrounding plants.

TRANSFORMATION OF MATERIALS AND ENERGY BY THE PLANT

Plants are composed of matter, and they absorb, store, and transform energy. Their very existence is dependent upon an exchange and transformation of materials and energy. Plants expend energy and do work. If it were possible to take moving pictures of all the parts of a growing plant, the film would show the roots twisting and turning and making their way about and between the soil particles. The young sprout of the germinating seed would be shown lifting the load of soil from its path and we could see the movement of the parts of opening buds. In fact, there is movement throughout the plant body although the rate of movement is generally slow. And if we examine the interior of the cells, we see the living material, the protoplasm, moving in streams from place to place in the cell. Thus plants, just as truly as animals, actually do work as long as they are alive, and this work requires a supply of energy.

Mention has already been made of the fact that if it were not for green plants none of the animals or chlorophyll-free plants in the world could exist. This is true because, with the exception of a few kinds of bacteria (see chemosynthesis on page 239) the chlorophyll-free plants and the animals are incapable of building up from the simple compounds in the soil and atmosphere the complex compounds of which their bodies are con-

structed. The formation of these complex compounds, or foods, constitutes the great rôle of green plants in organic nature. The making of foods by plants is of very great significance for two reasons:

1. Because these foods furnish the material out of which the bodies of plants and animals are constructed.

2. Because, in the making of these foods, energy from the sun, which is the world's great source of energy, is stored, and this stored energy can be released within the bodies of the living organisms which make or use the food. The energy thus secured is the only energy which animals or non-food-making plants can use for their life processes. In green plants it is the only energy which can be used for any process except carbohydrate manufacture. Since green plants are responsible for important transformations (1) of materials and (2) of energy, is fitting to summarize here these changes in material and energy.

The Material which Green Plants Absorb and the Changes which These Materials Undergo.—The principal substances which are taken into the green flowering plant in considerable quantity and which are essential to its proper development are as follows:

From the soil:

Water

Salts, containing the following elements:

Nitrogen—principally as nitrates but in some cases as compounds of ammonia

Phosphorus—as phosphates

Sulphur—as sulphates

Potassium

Calcium

Magnesium

Iron

} In combination with one of the three preceding elements

From the atmosphere:

Carbon dioxide

Oxygen

Nitrogen (perhaps)

The principal changes which these substances undergo in the plant will be briefly stated.

Water.—The water used in the process of photosynthesis is transformed, that is, it ceases to be water and becomes part of the carbohydrate, glucose. The water which passes from the plant during transpiration in the form of water vapor is changed only in its physical form and not (chemically) into another compound. During the process of respiration sugars are broken down and water is formed again.

Nitrogen, Phosphorus, and Sulphur.—These elements are particularly important as the raw materials, together with soluble carbohydrates, of the proteins and of the amino acids from which proteins are built up. Proteins contain from 15 to 19 per cent of nitrogen and from $\frac{1}{2}$ to $1\frac{1}{2}$ per cent of sulphur. It is said to be chiefly in the leaves that inorganic nitrogen is elaborated into amino acids and other nitrogenous organic compounds. Phosphorus is found in some proteins, particularly the nucleo-proteins of the nucleus, which contain from 0.3 to 3 per cent of that element.

Potassium, Calcium, Magnesium, and Iron.—Though all of the higher plants must be supplied with these substances, we have little knowledge of the changes which the simple inorganic compounds of these elements undergo within the plant. Part, at least, of the magnesium is used in the making of chlorophyll *a* and chlorophyll *b*. Iron is essential to chlorophyll formation, although the chlorophyll molecule contains no iron. Iron is also believed to act as a catalyst in the oxidation processes of plant respiration. It may be that potassium, calcium, and iron perform their essential function without change from the simple inorganic form in which they exist in the soil solution.

Carbon Dioxide.—Carbon makes up from 40 to 50 per cent of the dry weight of all plants, and the gas carbon dioxide is the source of all this carbon. The carbohydrates are utilized in the making of proteins and fats. When sugars and fats, which are

the principal respirable materials in the plant, are respired, carbon dioxide is again formed and liberated into the atmosphere. When plant parts die the sugars, starch, cellulose, fats, and all other organic compounds are broken down by bacteria and other fungi and the carbon is finally set free from these compounds in the form of carbon dioxide. Thus there exists in nature a carbon cycle in which the carbon of carbon dioxide is continuously being built up into complex foods, which are again broken down with the formation of carbon dioxide. Green plants, animals, and bacteria and other fungi may all play a part in this carbon cycle. (See page 239 and Fig. 153.)

Oxygen.—Carbohydrates, protein—in fact all essential substances in the plant—contain oxygen in combination with other elements. This oxygen is derived for the most part from water or from carbon dioxide used in photosynthesis. But the plant also absorbs the free oxygen of the atmosphere. This is utilized solely for the oxidation of sugars and fats in respiration and becomes part of the products of respiration.

Nitrogen.—Some simple green plants, such as some algae and certain bacteria, are able to use as nitrogen for protein manufacture the free nitrogen gas of the atmosphere. There can be no doubt that under natural conditions most of the nitrogen used in the formation of nitrogenous foods in the seed-bearing plants is secured from the soil in the form of compounds of nitrogen.

RÔLE OF THE ELEMENTS WHICH COME TO THE PLANT FROM THE SOIL

Element	Chief Rôles
<i>Nitrogen</i>	(a) Constituent of all proteins, which are essential components of protoplasm. (b) Lack of nitrogen results in a stunted plant. (c) Abundance of nitrogen tends to produce rank vegetative growth, and to retard the date of maturing of the plant.
<i>Phosphorus</i>	(a) Constituent of proteins, particularly those of the nucleus. (b) Transformation of insoluble carbohydrates into soluble

carbohydrates does not take place in absence of phosphorus.

- (c) Abundance of phosphorus tends to hasten the maturing of the plant and stimulates production of seed.

Potassium (a) Photosynthesis and translocation of carbohydrates are dependent upon the presence of potassium.

- (b) A deficiency of potassium is associated with a lack of carbohydrate reserve.

Calcium (a) Apparently stimulates root development.

- (b) A deficiency of calcium retards transportation of carbohydrates, and their utilization.

Magnesium (a) A component of the chlorophyll molecule; a deficiency of magnesium is attended by **chlorosis**.

- (b) Essential to formation of fats.

- (c) Aids in the transport of phosphorus from older to younger parts of the plant.

- (d) A deficiency of magnesium is attended by a reduction in fruit formation.

Iron (a) Essential to chlorophyll formation (not a part of chlorophyll molecule, however). A deficiency results in chlorosis.

Sulphur (a) Essential to the formation of proteins.

- (b) A deficiency of sulphur results in retarded cell division and suppression of fruit development.

In addition to the ten elements—carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, magnesium, calcium, and iron—long recognized as essential to the continued growth and development of green plants, there are certain other elements which are known to be beneficial or indispensable to some plants. For example, it has been found that **manganese**, **boron**, and **zinc** are essential to the growth of a number of different kinds of green plants, but that very small amounts suffice. Our failure to recognize earlier that certain of these elements are essential is due to two facts. First, that they are needed only in very small quantities and second, that the “chemically pure” compounds used in preparing culture solutions in the past have generally, or at least frequently, contained unsuspected traces

of these elements quite sufficient in quantity to supply the needs of the plant's growth in culture.

Other elements concerning which there is some evidence indicating their importance to particular plants are: **silicon, sodium, chlorine, aluminum, bromine, and iodine.**

Energy Changes Brought about by the Plant.—We have already learned that certain chemical changes, for example, burning and respiration, are attended by liberation of energy.

It is one of the principal rôles of green plants to take certain of the simple compounds (carbon dioxide and water) in which no available energy is stored and build them up into substances in which there is stored or potential energy. It is the energy of sunlight which is thus stored by green plants. These substances produced by plants constitute the source of all energy which is used by animals within their bodies, and by chlorophyll-free plants. Moreover, if we except the energy of falling water and of the wind, and that of the tides and waves, which we may some time be able to utilize, **all the energy which is used by man for any purpose is secured from the energy stored in the substances made by plants.** Our principal fuels, wood and coal, are unmistakably plant products. All the explanations of the origin of petroleum agree that directly or indirectly it also has been produced by green plants. The energy set free in the form of heat when these fuels are burned can be changed into mechanical energy by the steam engine or gasoline motor. This in turn may be transformed into electrical energy by the dynamo, and this again into light energy by the electric lamp or into heat by the electric stove. But whatever form it may take, the energy secured by the combustion of coal, wood, or petroleum is but the energy of sunlight which perhaps hundreds of centuries ago was absorbed by green leaves when carbon dioxide gas and water were being united to produce the energy-storing substances from which these fuels were formed. Green plants are then unique, not only as makers of substances essential for the building and repair of the bodies of all organisms, but also as the

stomers of the sun's energy for use within the bodies of organisms, and for use in the industries. The amount of energy which can be secured from other sources than the combustion of the products of photosynthesis is only a small fraction of that used in industry. Man is accordingly, and may always be, dependent upon green plants for much of the energy used in the industries, as he is also for all the energy used within his own body.

CHAPTER IX

THE PRINCIPAL PLANT GROUPS

Point of View.—We have discussed the form and structure of the various organs of the plants belonging to the Spermatophyta, or seed plants, the highest of the four divisions (see pages 3, 45 and 201) into which the plant kingdom is usually divided and have given an account of the physiological processes going on in these plants.

We shall now be concerned, for the most part, with the other three divisions of the plant kingdom, the Thallophyta, the Bryophyta, and the Pteridophyta. In our study of these plants and of two representatives of the Spermatophyta, we shall consider the following:

1. The probable course of evolution from the simplest plants through forms of increasing complexity to the seeds plants, which are the most highly organized of living plants.

2. The great variety in form and structure of the organisms making up the plant kingdom.

3. The peculiarities in structure, and particularly in function, by which many of the simpler plants manage to live successfully under conditions very different from those surrounding typical seed plants.

4. The importance of certain simpler plants, particularly the bacteria and other fungi, in relation to health, and to agriculture and other industries.

5. The principal laws of heredity and of evolution as illustrated by plants.

THE MEANING OF PLANT RELATIONSHIPS

There exist in the world today about a quarter of a million different kinds of plants which have been described and named,

and the number of named species of animals is much greater, nearly a million. New species are constantly being discovered by the systematic botanist and zoologist.

Among this great variety of different kinds of organisms there are many groups of species which obviously resemble each other more than they do any other kinds of organisms. Familiar examples of groups of similar species which are recognized even by those who are not given to accurate observations of plants are the oaks, all of which bear acorns and most of which have pinnately lobed leaves; the mints, which generally have square stems and whose foliage often has an aromatic odor; the beans, peas, and similar plants, whose fruits are pods or legumes and whose flowers are of a form which suggests a butterfly; and the toadstools and mushrooms with their stalked, umbrella-shaped caps. A careful comparison of the organisms about us would reveal many more such groups of strikingly similar species.

Both the existence of so many different kinds of organisms and the striking similarity between the members of such groups as have just been mentioned demand an explanation. One hypothesis is the **Theory of Special Creation**, which assumes that each species that exists or ever existed was separately created, and that each of the specially created individuals of a species was endowed with the power of producing other individuals like itself, but was without ability to give rise to individuals differing from it and thus to new species. This theory does not furnish any explanation of the close resemblances which exist between certain different kinds of organisms.

A second explanation is the **Theory of Organic Evolution**. This theory had its beginning as early as the time of the Greek philosophers, long before the beginning of the Christian era. Darwin was one among many scientists of his time who accepted the theory of organic evolution. His special service lay in his attempt to work out the factors in nature by which organic evolution has been brought about.

Evolution is a process in which great differences arise through a succession of slight changes. It is clear that such a process is

constantly going on among other things besides plants and animals. History is indeed merely an account of the evolution of human institutions, arts, and practices. Inorganic evolution (the evolution of other things than organisms) is illustrated by the collections, which may be found in many great museums, showing the history of the development of human apparel, implements of various sorts, optical instruments, etc. Within our own life many of us have witnessed practically the whole course of the evolution of the flying machine and of wireless communication. The geologist can inform us very fully in regard to the evolution of the hills, valleys, streams, and other features of the regions in which we live, and the astronomer knows much of the evolution of our earth and other planets and of the sun and stars.

It is, however, with the evolution of organisms (organic evolution) that we are here concerned. The now generally accepted explanation of the great number of plant and animal species, and of the close similarity existing between some of these, is called the Theory of Organic Evolution.

The principal features of this theory are briefly these:

1. The existing kinds of plants and animals and all the kinds that are now extinct, with the exception of one or a few original and very simple forms, have arisen from pre-existing kinds by relatively slow changes.

2. If the preceding proposition is true, it follows that all the different kinds of plants and animals are related.

3. Those species which are similar in many particulars are closely related, that is, they are not separated by many forms from a common ancestor (species) from which they have descended.

4. Although it is natural to look upon evolution as progressive, that is, as such that it results in an increase in complexity and differentiation, it may often be retrogressive and result in a development of forms having less complexity and differentiation than their ancestors.

If we could secure specimens of all the kinds of plants and

animals which now exist or which ever have existed, it should be possible by comparison of their structure to work out the whole course of evolution. Many species of plants and animals have become extinct. This extinction has in the case of a few species actually taken place since man has been studying plants and animals, and thousands of kinds of organisms died out before the animal species we call man was himself evolved. In the rocks we find the remains of some of these extinct plants and animals as fossils. These remains are in many cases mere fragments of the bodies of these organisms, and it is probable that fossil remains of many of these extinct plants and animals, particularly of the simpler and more primitive forms, will never be found.

CLASSIFICATION OF PLANTS

In spite of the fact that our knowledge of the extinct species, and of living species too, is very incomplete, it is possible for us to trace with considerable certainty the course of evolution within certain groups of related plants. Thus we arrive at a natural classification of such groups. Our conclusions in such cases are largely based upon a comparison of the structure and development of the plants or animals in question.

Comparison of the flower parts or of other structures connected with sexual reproduction is one of the most used and most dependable bases for judgment as to the relationship of plants. The vegetative structures of closely related plants may be adapted to very different environmental conditions and so may be dissimilar. Their reproductive structures, on the other hand, being shorter-lived, are subjected for shorter periods to environmental factors. In general, their relation to the environment is not so close and they are therefore less likely to change in response to differences in the environment. Reproductive structures are more conservative than vegetative organs and are therefore more dependable as indicators of relationship.

Other criteria used to determine relationship and therefore as bases for classification are: presence or absence of nuclei or

other characteristics of cell structure; arrangement of cells, i.e., singly, in pairs, filaments, sheets, or groups of various shapes; and presence or absence of certain vegetative organs and tissues.

Our knowledge of plants is too incomplete for us to work out a natural classification which will show the real relationships of all plants. Accordingly, the classifications of plants which we use are in part natural and in part artificial. One of the most widely used classifications is in part as follows:

A CLASSIFICATION OF THE PLANT KINGDOM

Rank	Scientific Names of the Groups	Common Names
<i>Division I</i>	<i>Thallophyta</i>	<i>Thallus Plants</i>
Subdivision 1	Algae	
Class 1	Cyanophyceae	Blue-green algae
Class 2	Chlorophyceae	Green algae
Class 3	Phaeophyceae	Brown algae
Class 4	Rhodophyceae	Red algae
Subdivision 2	Fungi	
Class 1	Bacteria	Bacteria
Class 2	Myxomycetes	Slime fungi
Class 3	Phycomycetes	Algal fungi
Class 4	Ascomycetes	Sac fungi
Class 5	Basidiomycetes	Club fungi
<i>Division II</i>	<i>Bryophyta</i>	<i>Moss Plants</i>
Class 1	Hepaticae	Liverworts
Class 2	Musci	Mosses
<i>Division III</i>	<i>Pteridophyta</i>	<i>Fern Plants</i>
Class 1	Filicineae	Ferns
Class 2	Equisetineae	Horsetails
Class 3	Lycopodineae	Club mosses and related plants
<i>Division IV</i>	<i>Spermatophyta</i>	<i>Seed Plants</i>
Class 1	Gymnospermae	Conifers and related plants
Class 2	Angiospermae	Higher flowering plants
Subclass 1	Dicotyledones	Dicotyledons
Subclass 2	Monocotyledones	Monocotyledons

The two groups (Algae and Fungi) into which the first division of the plant kingdom is subdivided are artificial groups based upon the manner in which these plants secure their food. The Algae are **autophytic**, that is, with few exceptions are able to carry on photosynthesis and are therefore independent of any other organisms. The fungi, on the other hand, are **heterophytic** and must, like animals, secure their food ready made, directly, or indirectly, from other organisms. Actually, however, some of the fungi are no doubt more closely related to some of the algae than they are to certain other species of the fungi, and certain algae are more closely related to certain fungi than they are to certain other algae.

CHAPTER X

THALLOPHYTA—ALGAE

CHARACTERISTICS OF THE THALLOPHYTA

THE name Thallophyta means thallus plants, a thallus being a plant body without true roots, stems or leaves. There are, however, thallus plants in other divisions besides the Thallophyta, and in some plants belonging to the Thallophyta there are structures which resemble superficially the roots, stems, and leaves of the flowering plants and which perform the same functions, at least in part.

The thallophytes include a great variety of plants which have little in common, save the small size and simplicity of most of them. Typically the Thallophyta are aquatic plants, but many of the fungi, though preferring moist locations, do not thrive if submerged in water.

Reproduction in the thallophyta (as in the other divisions) may be either by the asexual or the sexual method. In the former method each new individual is the product of a single parent plant, while in the sexual method each new individual develops from a cell (the **zygote**) which is the product of the fusion of two protoplasts generally originating in different parent individuals.

Asexual Reproduction by Fission.—The simplest form of asexual reproduction is called **fission**. It is restricted to unicellular organisms and is the sole method of reproduction employed by the most primitive plants. It consists merely in the division of a single-celled individual into two protoplasts of equal size. These two new individuals, produced by fission, together contain all the materials of the single parent cell. Organisms

which reproduce solely by this method, therefore, never die except as the result of shortage of food or water or other unfavorable external conditions.

Asexual Reproduction by Spores.—Asexual spores may be either non-motile or capable of active locomotion by means of whip-like filaments of protoplasm called cilia (singular, cilium).

The motile asexual spores are called zoospores. There are other motile cells produced by plants, but zoospores are the only motile protoplasts that are able to develop directly into new individuals. Zoospores do not have any cell walls but simply consist of a naked mass of protoplasm. In some cases the entire protoplast of a vegetative cell escapes as a single zoospore; in other cases the protoplast of a vegetative cell divides into two or more protoplasts, each of which develops one or more cilia and becomes a zoospore.

Non-motile asexual spores often consist of a vegetative cell which has grown in size and thickened its wall. In other cases the non-motile asexual spores are special cells and are produced within an organ called a sporangium.

Sexual Reproduction.—The protoplasts which fuse to form the zygote in the process of sexual reproduction are called gametes (Figs. 133 and 134). They are almost always naked protoplasts, having no cell wall. In the blue-green algae, in many other simple algae, and in the bacteria there is no sexual reproduction. In most primitive cases of sexual reproduction in plants the gametes are all alike in size and structure. Such gametes are called isogametes. They are generally motile, having cilia, like zoospores. The gametes are, however, usually unable to produce new individuals until they have fused in pairs. It is customary to speak of the fusion of isogametes as conjugation, and of the resulting zygote as a zygospore. The protoplast of the zygospore forms around itself a cell wall which generally becomes thickened and thus protects the protoplast within. The zygospore in most species remains in a resting condition for some time before it germinates and gives rise to new plants.

Most Thallophyta and other plants having sexual reproduction do not have isogametes but produce two kinds of gametes — **heterogametes**. These heterogametes may differ merely in size, the smaller, ordinarily, being more active than the larger. Generally, however, the larger gametes are without cilia and therefore incapable of locomotion. The smaller, active gametes, which are called **male gametes**, or **sperms**, are produced in much greater numbers than the larger female gametes, which are known as **egg cells** (Fig. 138). In plants which produce heterogametes the zygote is formed by the fusion of a male gamete or sperm, with a female gamete, or egg cell, and never by fusion of two gametes of the same sort. The process of fusion of heterogametes is called **fertilization** and the resulting zygote an **oospore**.

Oospores generally become surrounded by a thick wall, as do zygosporcs, and in most cases do not germinate and develop into new plants until after a period of dormancy. Zygosporcs, oospores, and asexual spores generally germinate in much the same manner. If they are resting spores, capable of remaining dormant for some time, their protoplasm generally contains much less water than does active protoplasm. When the conditions for germination are favorable, water is absorbed through the spore wall by the enclosed protoplast. The resulting swelling of the protoplast ruptures the spore walls, and a part of the protoplasm extrudes through the opening. The protoplasmic projection soon forms an enclosing cell wall which, with the contained protoplasm, is called the **germ tube**. This tube continues to grow, and in most cases its contents divide to form a number of cells from which the new plant develops.

It is obvious that each zygosporc, of such forms as *Spirogyra*, and each oospore, of such heterogamous plants as *Oedogonium*, contains chromatin derived from the male and female gametes, and thus has twice as many chromosomes as the nuclei of the vegetative cells. In all plants having sexual reproduction there is such a doubling of the chromosome number when the zygote is formed. At some stage in the life history of such plants, there

is necessarily a reduction in the number of chromosomes from the $2x$ or **diploid** number to the x or **haploid** number. This reduction division takes place at different points in the life history of different plants. In *Spirogyra*, for example, the nucleus of the zygospore very promptly undergoes division and the resulting daughter nuclei again divide, so that the zygote has four nuclei. Three of these nuclei disintegrate, so that the mature zygote has but a single nucleus. One of the early nuclear divisions is a **reduction division**, in which the chromosome number is reduced to the normal number for ordinary cells of the species. In *Oedogonium* four zoospores are developed from each oospore, and one of the two divisions which results in the formation of these four zoospores is a reduction division, so that the resulting nuclei have half the number of chromosomes which appear at the first division of the zygote nucleus.

The following is a summary of methods of reproduction in the Thallophyta, and indicates the spore types involved.

Asexual Reproduction (without union of protoplasts)

- (I) Fission—division of single-celled individual into two new unicellular individuals of equal size. (Fig. 127).
- (II) Asexual spore formation.
 - (1) Motile asexual spores—zoospores (Figs. 133 C and 137).
 - (2) Non-motile asexual spores (Fig. 130)

Sexual Reproduction (with union of protoplasts)

- (a) Conjugation—the fusion of similar gametes (isogametes) to form a zygospore (Figs. 133 E, F and G, 134).
- (b) Fertilization—the fusion of dissimilar gametes (heterogametes) to form an oospore (Figs. 138, 147A).

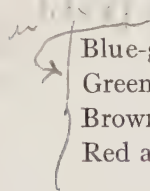
ALGAE (AUTOPHYTIC THALLOPHYTA)

Characteristics of the Algae.—With very few exceptions, the algae possess chlorophyll, although many of them, particularly

the red algae and the brown algae, are not green in color because of other pigments which are associated with the chlorophyll and mask its green color.

The great majority of algae are aquatic, though some grow on soil and a few others on the stems of trees or upon other objects exposed to the air. Algae make up the greater part of the vegetation of the ocean, and are also common in bodies of fresh water. There is a great range of size and complexity among the algae.

The Four Classes of the Algae.



Blue-green algae	(Cyanophyceae)
Green algae	(Chlorophyceae)
Brown algae	(Phaeophyceae)
Red algae	(Rhodophyceae)

The names of the four classes of the Algae are based upon the characteristic differences in color. However, the color differences are not the sole nor the most important ones. The members of each class have certain characteristics in common, such as cell structure, reproductive processes, etc., which in general are more dependable as indicators of relationship than is color. There are in fact some Cyanophyceae which are brown, some Chlorophyceae which are red, and some Phaeophyceae and Rhodophyceae which are green.

THE CYANOPHYCEAE—BLUE-GREEN ALGAE



Characteristics of the Cyanophyceae.—The plants of this class are made up of cells which are without definite nuclei and, with few exceptions, without any distinct chloroplasts. The pigments of the cells are generally restricted to the outer region of the protoplast, but this colored part is not sharply marked off from the colorless protoplasm within, which is called the central body. The central body has been called an “incipient nucleus,” and may represent a stage in the evolution of a true nucleus. It

probably contains in all cases granules of a material similar to

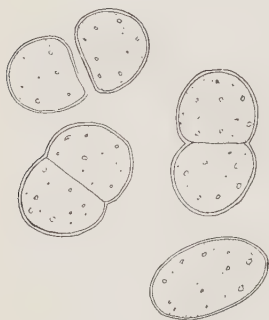


FIG. 127.—*Synechococcus*. A blue-green alga the cells of which are solitary except during fission. Several stages of fission are shown as well as a single cell almost ready for division.

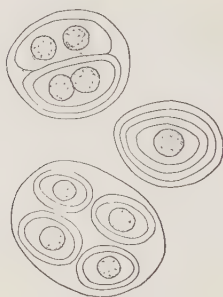


FIG. 128.—*Gloeocapsa*, blue-green alga the cells of which occur generally in groups, the cells formed by the fission of a single cell being held together by the gelatinous coating of the cell from which they came.

the chromatin of the nuclei of most plants. The cell walls of the

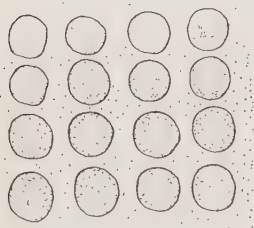


FIG. 129.—*Merismopedia*, a blue-green alga the cells of which are held together by a gelatinous matrix. The cells divide in two planes only and as a result the groups of cells have the form of flat plates. These may grow to considerable size and consist of scores of cells.

Cyanophyceae consist, as a rule, not of a carbohydrate, cellulose, but of chitin, a nitrogen-containing substance which is found in the cell walls of bacteria and in many animals, particularly insects. In addition to chlorophyll the plants of this group generally contain one or more accessory pigments, the commonest of which is a blue pigment called **phycocyanin**. A red accessory pigment is present in some forms, so that there are "blue-green" algae which are red and which may give a bright red color to water when present in large quantities. Almost all Cyano-

phyceae secrete considerable quantities of a gelatinous substance which forms a sheath or matrix around the cells or cell groups.

The product of photosynthesis in the Cyanophyceae is not starch or glucose but another carbohydrate, **glycogen**, which is also found in many fungi and frequently in animals.

There is **no sexual reproduction** in the Cyanophyceae.

Distribution of the Cyanophyceae.—These plants are abundant in fresh and in brackish water and in water contaminated

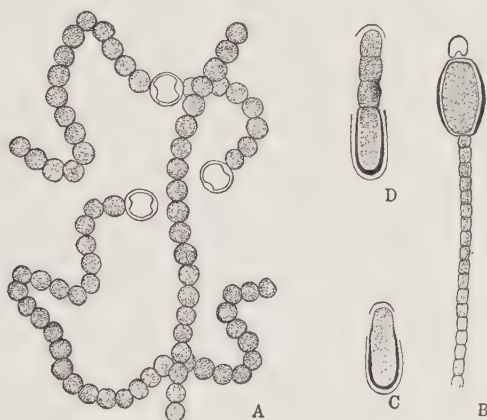


FIG. 130.—*A*, *Nostoc*, filament showing heterocysts; *B*, *Cylandrospermum* filament showing heterocyst and thick-walled resting spore; *C* and *D*, germinating resting spores.

by sewage, and many forms are found in the sea. A number of forms are abundant in moist soil, especially when it is rich in organic matter; on trunks and branches of trees; and on rocks. They form the principal vegetation of hot springs, where they have been found living in water as hot as 87°C .

Representatives of Cyanophyceae.—The simplest members of this group, such as *Synechococcus* (Fig. 127), consist of single cells which are generally spherical or oval. These single cells which constitute the plant body are capable of carrying on all essential life processes. They generally live either immersed in

water or in very moist habitats where they are wet most of the time. Through the surface of the cell the protoplast absorbs water, inorganic salts, and the gases, carbon dioxide and oxygen. By photosynthesis the protoplast forms carbohydrates which, as in the higher plants, are used in part for respiration and in part for the formation of substances from which new protoplasm can be built up.

In some forms, such as *Gloeocapsa*, the daughter cells, resulting from fission, are held together by a gelatinous matrix in groups of two, four, eight, or more cells, each cell, however, being entirely independent of the other cells of the group.

In other forms, as *Nostoc* and *Oscillatoria*, the cells resulting from a succession of fissions remain attached and form chains or filaments. In *Nostoc* many hundreds of these filaments are held within a gelatinous mass produced by the cells. Here and there in the *Nostoc* filaments, large, colorless cells, called **heterocysts**, occur. The filaments break apart easily at these heterocysts, forming short filaments, capable of locomotion and known as **hormogonia**, which grow into long filaments by growth of and division of their cells. Hormogonia are formed in *Oscillatoria* by the death of a cell or group of cells here and there in the filament. The filaments of *Oscillatoria* can move from place to place, exhibiting a swaying or oscillating as well as a twisting or rotating movement.

Nostoc shows a slight advance over such forms as *Oscillatoria* in the formation of resistant cells, or asexual spores from some of the ordinary vegetative cells. These spores



FIG. 131.—A portion of a filament of *Oscillatoria*, one of the commonest blue-green algae. The divisions of the cells take place in parallel planes so that the cell groups are filamentous and unbranched. As the result of the death of a cell here and there, the filament breaks up into short pieces called hormogonia.

germinate to form new filaments when conditions become favorable.

Nostoc and *Oscillatoria* are probably to be considered rather as colonies of unicellular plants than as multicellular individuals, although the distinction between these two states is not a very sharp one.

THE CHLOROPHYCEAE—GREEN ALGAE



Characteristics of the Chlorophyceae.—All of the plants included in this group have chloroplasts and a definite nucleus. These two characteristics distinguish the Chlorophyceae from the blue-green algae but not from the red or brown algae. Most of the green algae possess in their cells only the pigments which are typically present in green cells—chlorophyll *a* and chlorophyll *b*, carotin, and xanthophyll. The cell walls are not chitinous but with few exceptions consist mostly of cellulose. In most of the green algae starch is the first visible product of photosynthesis, although some produce no starch and have oil as the only visible product of photosynthesis.

Distribution of the Chlorophyceae.—Members of this group are found in nature in almost every conceivable moist place where the temperature is not very high and where light can penetrate. The larger number are fresh-water plants; while relatively few are marine. Most of the latter occur in tropical seas. There are a number of green algae which are commonly found in soil very near the surface, and a few, such as the common *Protococcus*, on the bark of trees or attached to fence posts or other objects. Some green algae grow in association with certain fungi, forming what are known as lichens.

Representatives of the Chlorophyceae.—One of the simplest of the green algae is *Protococcus*, probably the commonest, most widely spread green alga in the world. It forms a coating on the shaded and therefore more moist side of the branches and trunks of trees, rocks and fence posts. It may occur singly, or in groups of two or four individuals. These unicellular plants are

entirely independent, carrying on all essential life processes within the single cell. Reproduction is asexual, occurring by fission only.

A more complex type is *Ulothrix*, an unbranched, filamentous alga, in which the basal cell of the filament is specialized to form a **holdfast** (Fig. 133). Here is a simple case of specialization of one cell of a group for a function not performed by other cells of the group. In this we have what seems to be the beginning of the

development of the multicellular type of plant as distinct from the strictly unicellular and the colonial type.

Ulothrix reproduces both asexually and sexually. In the former case the protoplasts of some or all of the cells of a filament may contract, round up, and develop cilia, each protoplast thus forming from one to eight motile, asexual spores, known as zoospores, each capable of forming a new plant. The zoospores bear four cilia each.

Ulothrix reproduces sexually by the production of motile gametes.

It has the most primitive type of sexual reproduction, as the gametes are alike in size and structure and are therefore isogametes. Their fusion in pairs is known as conjugation, and results in a heavy-walled zygospore.

The development of the gametes in *Ulothrix* is very similar to the process of zoospore formation. The gametes arise from divisions of the protoplasts of the cells of the filament, but are generally smaller than the zoospores, a single cell often giving rise to as many as sixteen or thirty-two gametes. Each of the gametes has two cilia instead of four as in the case of the zoospores.

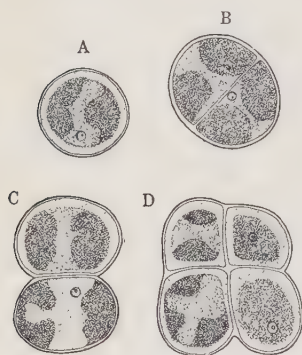


FIG. 132.—*Protococcus*, a simple green alga, in which the cells remain united for some time after fission, forming groups of varying size and cell number.

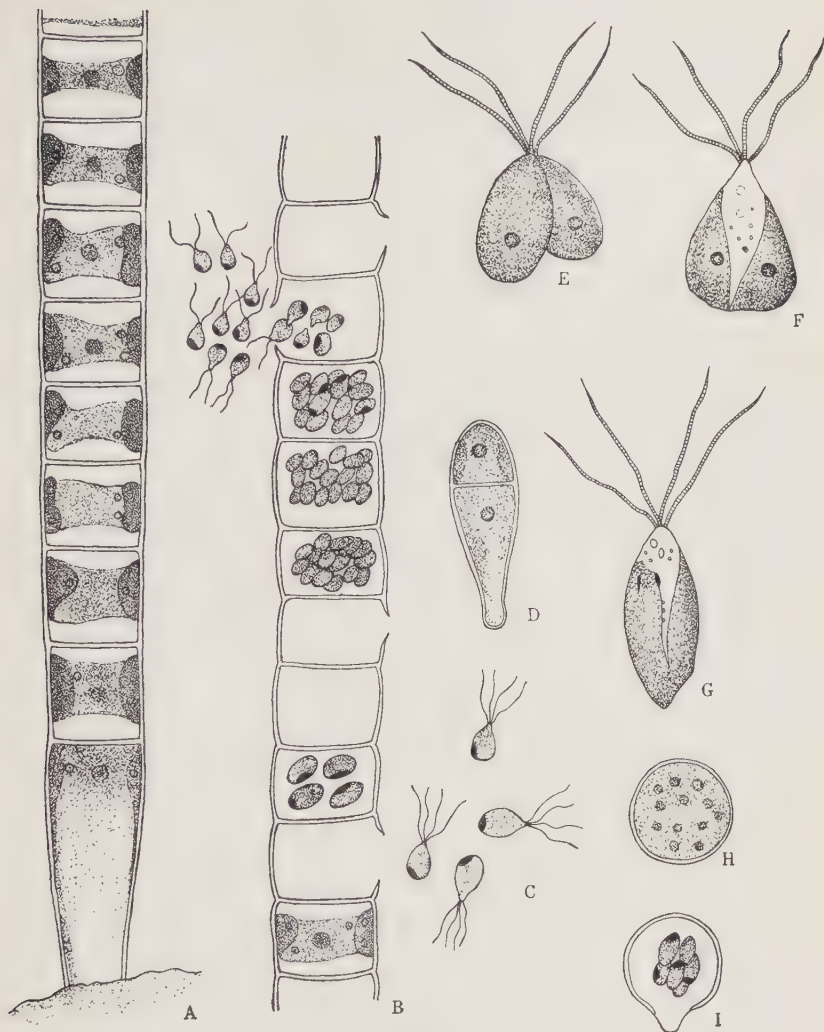


FIG. 133.—*Ulothrix zonata*. A, a portion of a filament showing the holdfast cell at the base, and the ordinary vegetative cells. B, a portion of a filament which is forming gametes (above) and zoospores (below). These can be distinguished by the fact that gametes bear two cilia each and the zoospores four. C, a number of zoospores which have just escaped. D, a germinating zoospore. E, F and G, stages in the conjugation of gametes. H, a zoospore in the resting condition. I, germinating zoospore showing the division of its protoplast into a number of zoospores. (E-H after Oltmanns.)

The zoospores give rise to new filaments directly, whereas the protoplast of each zygospore, on germination, divides to form a number of zoospores which then produce new filaments. Zoo-

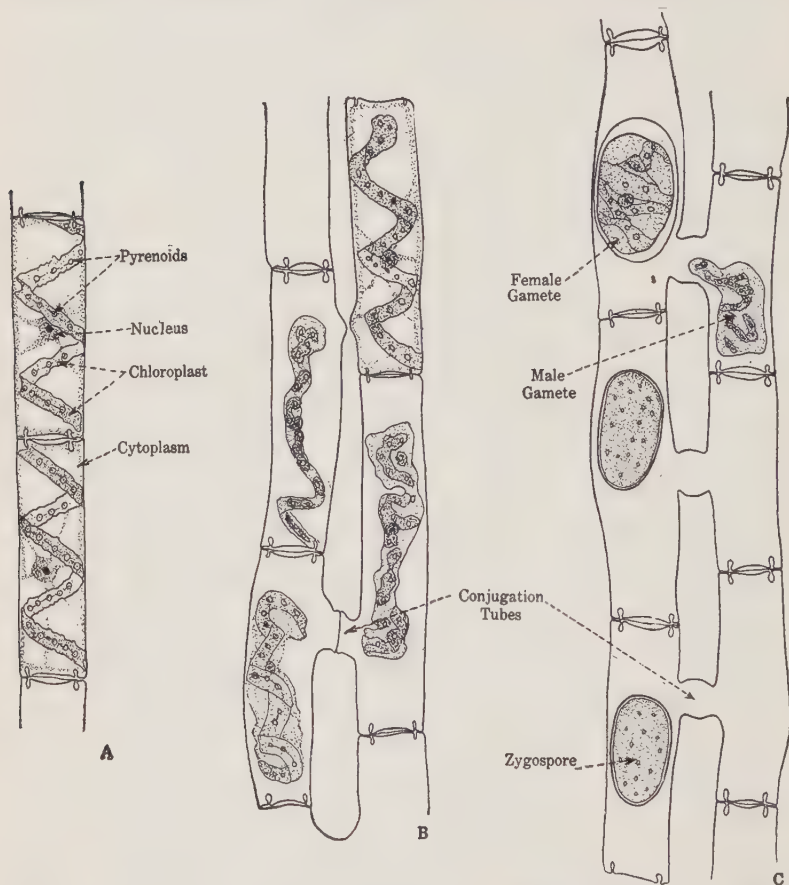


FIG. 134.—*Spirogyra*. To the left two cells from a filament which is in the vegetative condition. The other two figures show successive stages in scalariform conjugation, that is between the cells of two adjoining filaments.

spores are not resistant to unfavorable conditions, as they are naked protoplasts, but zygospores may be very resistant, due to heavy walls.

Some of the Chlorophyceae, such as *Spirogyra*, develop no zoospores or other non-sexual spores. In this plant the filaments elongate, as do those of the *Cyanophyceae*, by simple division of the

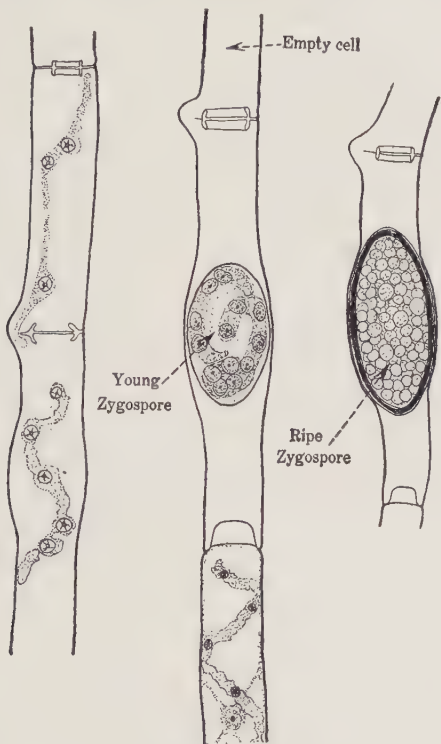


FIG. 135.

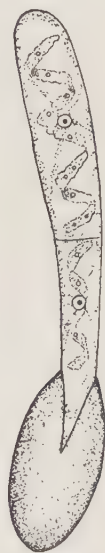


FIG. 136.

FIG. 135.—*Spirogyra*, showing three stages in lateral conjugation. In this case conjugation is between adjacent cells of the same filament. In the filament on the left only the chloroplast of the two conjugating protoplasts (gametes) are shown.

FIG. 136.—Germination of a zygospore of *Spirogyra*.

component cells. Isolated portions of filaments may thus grow to form new filaments, suggesting the hormogonia production of *Oscillatoria* and *Nostoc*. The protoplasts of ordinary vegetative cells act as gametes, and since these gametes are structurally

alike they are isogametes. Conjugation of the protoplasts of two adjacent cells of the same filament may occur. More commonly conjugation takes place between protoplasts of different filaments. Usually the protoplasts of one filament remain passive, while the protoplasts of the adjoining filament pass over through connecting tubes. This difference of motility may be considered one of the first indications of sexual differences in gametes.

Oedogonium is a common green alga showing a greater degree of differentiation than any form thus far mentioned. It repro-

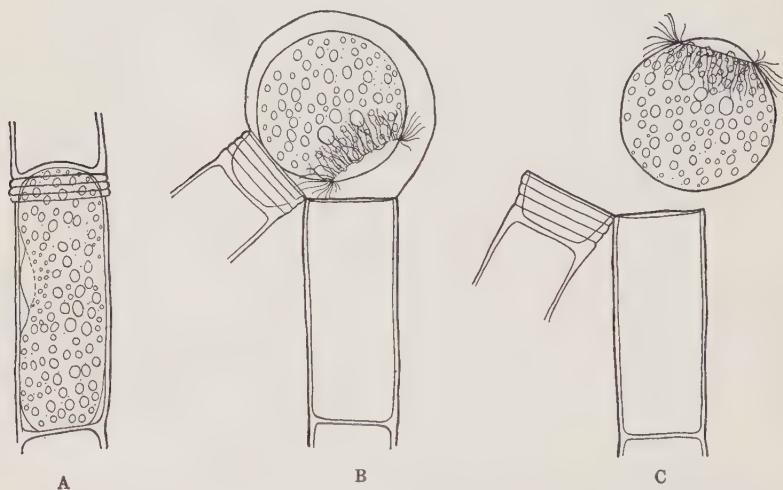


FIG. 137.—Formation and escape of a zoospore in a species of *Oedogonium*. (Re-drawn from Hirn.)

duces by means of zoospores and also by heterogametes. The basal cell of the filament forms an organ of attachment, or holdfast. Not all the cells in the filament are able to divide and thus add to the length of the filament; certain cells alone have this power. Gametes are not produced in ordinary vegetative cells, as in *Ulothrix* and *Spirogyra* but in special organs called **gametangia**, much different in form from the vegetative cells although developed from them. On account of

this considerable physiological division of labor, *Oedogonium* is certainly to be considered as a multicellular plant.

In most species of *Oedogonium* each zoospore consists of the entire protoplast of a vegetative cell. The zoospores are provided with a ring or collar of cilia around the colorless forward end.

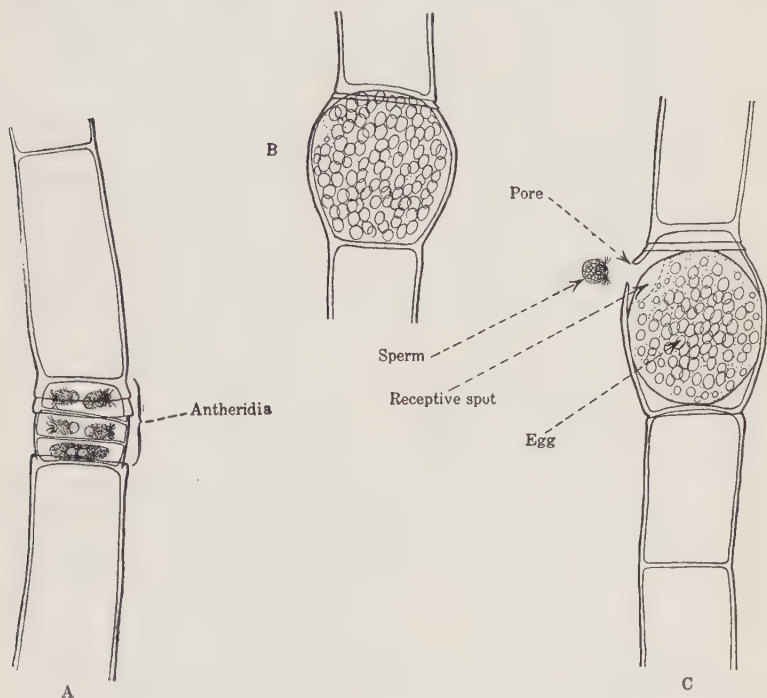


FIG. 138.—*Oedogonium*. A, portion of a male filament showing several antheridia. B, an immature oogonium. C, part of a female filament showing a ripe oogonium, the egg cell of which is about to be fertilized. For the ripe oospore and the structure of a vegetative cell, see Fig. 139A. C, somewhat diagrammatic.

Generally only a few cells of a filament produce these motile spores.

The male gametes, or sperms, of *Oedogonium* are produced in short cylindrical cells, the **antheridia** or male gametangia, and are much smaller than the female gametes, or eggs. The latter are

without cilia and remain within the female gametangium or oogonium until after fertilization. The sperms are like miniature zoospores in form and are produced, in much larger numbers

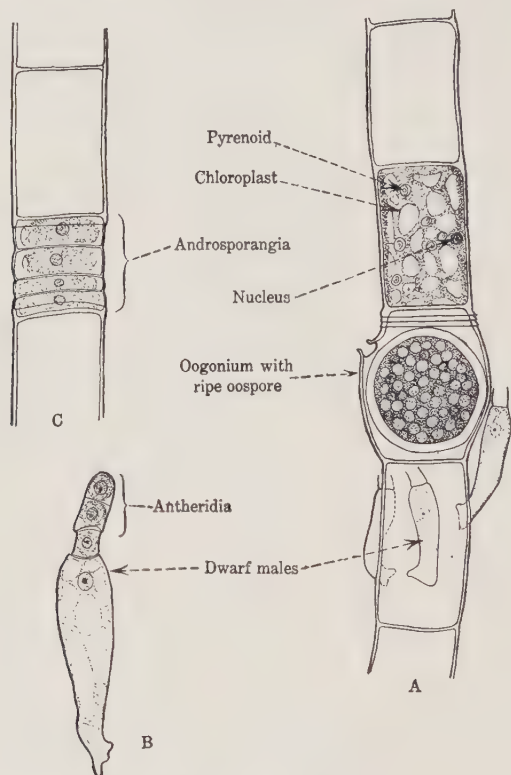


FIG. 139.—A species of *Oedogonium* which produces dwarf males. A, portion of an oogonial filament showing the structure of a vegetative cell, an oogonium containing a ripe oospore and three dwarf males which have discharged their sperms. B, a single dwarf male showing the holdfast cell at the base and the antheridia. C, a portion of a filament with androsporangia within which are developing androspores (zoospores which germinate and give rise to dwarf males).

than the egg cells, in the same or in different filaments. The oogonia are spherical or oval cells. After the development of the egg a pore is formed, through which the sperm may enter, by

the dissolution of a small area of the oogonium wall. Almost immediately after the entrance of the sperm into the egg, a thick wall is formed about the zygote or oospore. Decay of the oogonium wall releases the oospore, which is resistant to conditions unfavorable to the vegetative cells, as are the zygospores of *Ulothrix* and *Spirogyra*. The oospore does not produce a new plant directly but its protoplast divides to form four zoospores which in turn give rise to the new filaments. The striking similarity between the sperms and zoospores distinctly indicates the possibility of the origin of gametes from zoospores.

Systematic botanists have divided the Chlorophyceae into a number of smaller groups, each of which seems to have evolved independently from some ancestors belonging to a single group of simple organisms, probably the flagellates. Within several of these smaller groups it is possible to find series of genera which indicate the development from very simple forms without sexual reproduction, through forms of more complexity and with

isogamous sexual reproduction, to heterogamous, larger and still more complex forms in which the gametes are distinctly differentiated. It appears that among these plants there has been, at least in several of the smaller groups, a parallel development from very simple to more complex plant bodies, and that sexual reproduction and the development of heterogamy has taken place independently in each of these different groups.

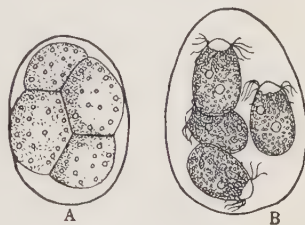


FIG. 140.—Germination of oospore of *Oedogonium*. A, the protoplast of the oospore dividing into four protoplasts. B, the four zoospores formed from the four protoplasts. The oospore has a nucleus with "2x" chromosomes, the zoospores having nuclei with "x" chromosomes.

(THE PHAEOPHYCEAE—BROWN ALGAE)

Characteristics of the Phaeophyceae.—The third class of the algae, the brown algae or Phaeophyceae, includes the largest and

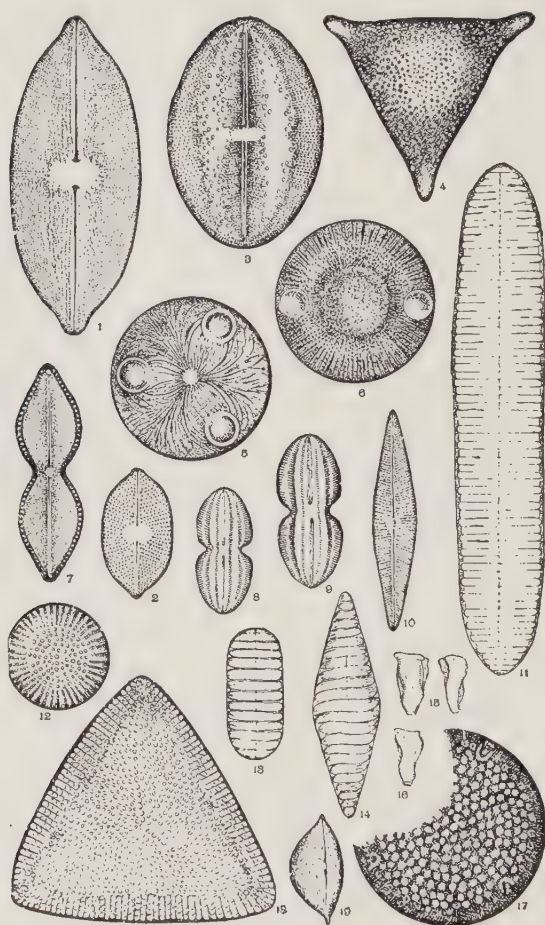


FIG. 141.—Diatoms (all highly magnified) showing various forms and markings. The diatoms are a remarkable group of algae found for the most part floating in bodies of fresh water or in the sea. Such large quantities of silica are present in their cell walls that these microscopic plants are very perfectly preserved as fossils. Deposits of fossil diatoms thousands of feet thick exist in several parts of the earth.
(From Wolle's *Diatomaceae of North America*.)

the most highly differentiated of the thallophytes as well as some forms of small size and very simple structure. The range of size is from species which are microscopic to such genera as *Macrocystis* which may attain a length as great as 200 meters, the



FIG. 142.—Structure and reproduction of a species of *Ectocarpus*. *A*, habit drawing. *B*, a portion of a plant showing zoosporangia. *C*, a single gametangium and vegetative cells. *D*, portion of a plant showing gametangia. *E*, two zoospores. *F*, several stages in conjugation, including a zygospore, to the right of the letter.

G, two gametes about to conjugate. (*A* to *D* after Setchell and Gardner.)

latter form no doubt exceeding in maximum length any other organism now living. No unicellular organisms are found in this group. All the Phaeophyceae have cells with definite nuclei and distinct plastids. These latter contain, in addition to chlorophyll *a*, chlorophyll *b*, carotin, and xanthophyll, a brown accessory

pigment, called **fucoxanthin**, which usually entirely hides the green color of the chlorophyll. All of the brown algae normally grow attached but plants may become detached and still survive. In the Phaeophyceae no resting spores are produced, and all motile cells, whether zoospores or gametes, have two cilia which are laterally attached.



FIG. 143.—A large kelp (*Pelagophycus*) from the Californian coast. (Photograph furnished by W. A. Setchell.)

Distribution of the Phaeophyceae.—These plants are much more common and better developed in the cool ocean waters of the temperate zones than in warm tropical seas. Only a few species are found growing in fresh water.

Representatives of the Phaeophyceae.—*Ectocarpus* is a form which, like *Ulothrix*, illustrates the probable origin of sexual reproduction. The gametes are similar to zoospores in structure

but normally do not develop new plants without fusion to form a zygospore. Among the different species of *Ectocarpus* there are apparently the beginnings of a differentiation of gametes. In some forms there is a slight difference in size, and it is said that in such cases only gametes differing in size are able to fuse. In some other species, in addition to size differences, there is also said to be a difference in degree of motility, the larger gametes

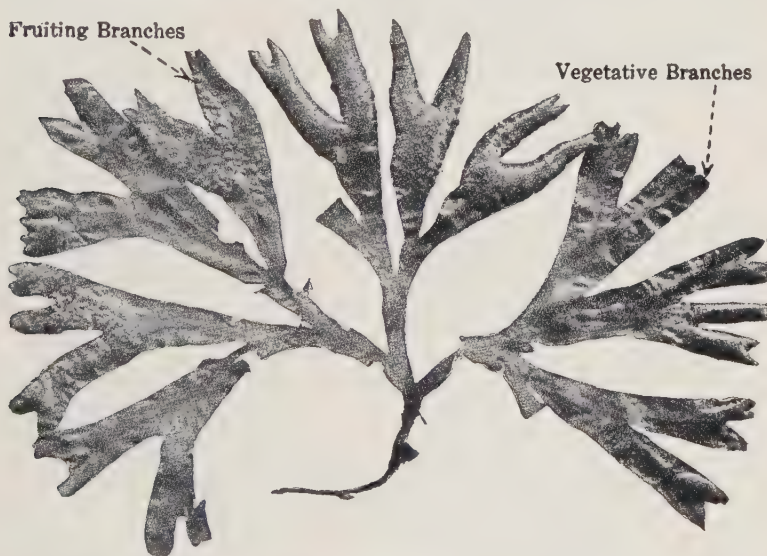
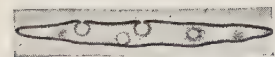


FIG. 144.—A frond of a species of *Fucus*, showing the dichotomous method of branching, vegetative branches, and fruiting branches with numerous conspicuous swellings (openings of the conceptacles). (Photograph furnished by Gardner and Setchell.)

moving less actively and coming to rest earlier than do the smaller ones which fuse with them as they become quiescent. In short, little distinction seems to exist in the genus *Ectocarpus* as a whole between zoospores and gametes, and there occur various gradations between isogametes and heterogametes.

The kelps include those plants which form the extensive kelp beds off the Pacific coast, some of the plants, such as *Macrocystis*, being several hundred feet in length. They possess a holdfast, or

**A****B****C****D**

organ of attachment, which superficially resembles a root system, a stalk or stipe, and expanded blade-like portions which strongly suggest the leaves of the spermatophytes. There is also a considerable differentiation of tissues.

In the kelps a condition known as **alternation of generations**, which also exists in certain Rhodophyceae and which is the rule in all the Bryophyta, Pteridophyta, and Spermatophyta. The zoospores which are formed, upon germination give rise to very small plants quite unlike the typical kelp plants on which the zoospores were borne. These minute plants are of two sorts, antheridial and oogonial, producing respectively sperms and eggs. The sperms and eggs fuse forming zygotes which on germination, develop into typical kelp plants. Thus there is a gamete-producing

FIG. 145.—A dioecious species of *Fucus*. *A*, cross section of a fruiting tip of a male plant, showing the compact outer region (the cortex), the loose tissue within (the medulla), and several antheridial conceptacles. *B*, a single antheridial conceptacle in section showing the opening to the surface (the ostiole) and the antheridial-bearing hairs which arise from the inner surface. *C* and *D*, antheridia and the branched hairs upon which they are borne. (After Thuret.)

generation (**gametophyte phase**), the nuclei of which have the haploid chromosome number, alternating with a generation (**sporophyte phase**) which produces asexual spores with diploid nuclei.

Fucus is a brown alga which also shows considerable complexity of the plant body and much differentiation of tissues as compared with the blue-green and green algae. There is a distinct differentiation of gametes, the sperms being very small in size, highly motile and produced in very great numbers, whereas the eggs are large (the volume may be as much as thirty thousand times as great as that of a sperm), relatively few in number, and without power of locomotion. The eggs are expelled from the oogonia and fertilization occurs outside in the sea water. The resulting zygote does not produce a thick wall and become a resting spore

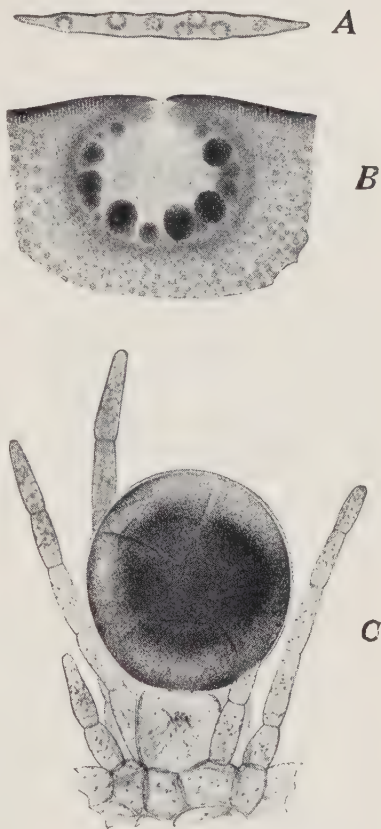


FIG. 146.—A dioecious species of *Fucus*. *A*, a cross section through a fruiting branch of a female plant showing the cortex, medulla, and several oogonial conceptacles. *B*, a single oogonial conceptacle in section, showing the ostiole and the oogonia and paraphyses which line the conceptacle. *C*, a portion of the floor of the conceptacle showing an oogonium attached by its stalk cell and surrounded by a number of paraphyses. Note that the protoplasm of the oogonium has undergone cleavage to form the eight eggs which have not yet rounded up. (After Thuret.)

but germinates at once to produce a new plant like the one which bore the gametes which gave rise to it.

THE RHODOPHYCEAE—RED ALGAE

Characterics of the Rhodophyceae.—The fourth class of the algae is made up of plants which are mostly marine, although a few species live in fresh water. All members of this class are multi-

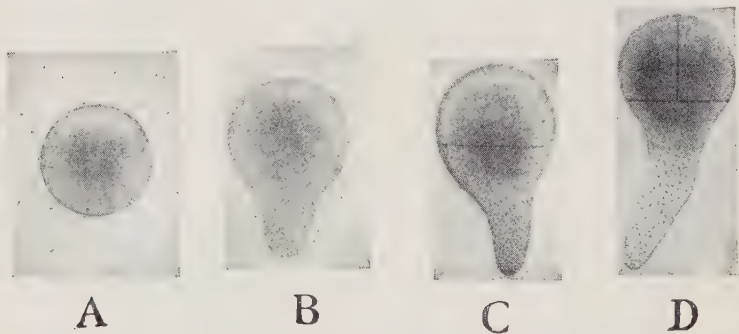


FIG. 147.—Fertilization of the egg and germination of the oospore of a species of *Fucus*. A, an egg surrounded by many sperms. B, an oospore germinating. The tubular outgrowth, which later forms a holdfast at the tip, arises always on the side of the oospore away from the light. C, the young plant has divided into two cells by a transverse wall. D, a wall at right angles to the first divides the upper of the cells into two cells. (After Thuret.)

cellular. In general they are clearly more differentiated than the green algae, but as a group are characterized by simpler structure than the kelps and *Fucus*. Most of the vegetative cells have a single nucleus, and the plastids, which may occur in large numbers in each cell, contain in addition to chlorophyll *a*, chlorophyll *b*, carotin, and xanthophyll, an accessory pigment called **phycoerythrin**. True starch is never found in the Rhodophyceae, but grains of a reserve carbohydrate, which stains red instead of blue when treated with iodine, are often present.

In many red algae the cell walls are very thick, so that the protoplasts appear to be embedded in an extensive gelatinous

matrix. Some of these plants, which have a finely branched plant body, are certainly to be considered the most delicate and beautiful of all marine plants. In one group of red algae, the coralline algae, the cell walls become encrusted with large quantities of carbonate of lime and are strongly suggestive of corals.

No ciliated cells have been found in the red algae. Sexual reproduction is always heterogamous, and the life history of these plants is usually rather complicated, involving in many species an alternation of asexual and sexual generations.

Distribution.—The Rhodophyceae are abundant in the temperate seas, but the number and variety of forms are greater in the warmer tropical and subtropical waters. They are generally found below low-tide level and may grow at depths as great as 200 meters.



FIG. 148.—A portion of a red alga, *Pterosiphonia*, a genus closely related to *Polysiphonia*. (Photograph furnished by N. L. Gardner.)

RELATIVE COMPLEXITY OF ALGAE AND TYPICAL LAND PLANTS

Such complexity as is characteristic of typical land plants is not found in the algae, not even in the great kelps. The relatively small number of organs and slight differentiation of tissues in the algae are sufficient for successful existence in the comparatively uniform environment of the water habitat. The plants, being

largely supported in the water by their buoyancy, have less need for mechanical tissues than plants which grow erect in the air. Special tissues for absorption and conduction are less needed than in the case of land plants, since the immersed algae are entirely bathed in water, which supplies the necessary mineral salts, carbon dioxide for photosynthesis, and oxygen for respiration. Tissues for the regulation of water loss are obviously entirely unnecessary.

CHAPTER XI

THALLOPHYTA—FUNGI

THE fungi do not constitute a natural group for among them are included plants which are certainly more distantly related to each other than they are to certain plants outside the fungi. The single definite basis of distinction between the algae and the fungi is the fact that the algae can make their own food from simple inorganic food materials, whereas the fungi, lacking chlorophyll, must secure their food ready made from some other living organisms or from the dead remains or products of some organism.

An organism deriving its food from the living body of either a plant or an animal is termed a **parasite**. An organism obtaining its food from the dead body or the non-living products of another plant or animal is called a **saprophyte**.

In the condition called parasitism, one organism, the parasite, secures its food entirely or in part from the tissue of another living organism, known as the **host**. The parasite contributes nothing to the advantage of the host.

We shall consider the fungi as consisting of the following five groups:

- Class 1.—The Schizomycetes or Bacteria (Fission Fungi).
- Class 2.—The Myxomycetes (Slime Fungi).
- Class 3.—The Phycomycetes (Algal Fungi).
- Class 4.—The Ascomycetes (Ascus Fungi).
- Class 5.—The Basidiomycetes (Basidium Fungi).

These five classes include all the parasitic or saprophytic plants except a relatively small number which show by their

structure and development that their closest relatives belong to one of the great groups of autophytic plants.

BACTERIA

General Characteristics.—The bacteria are strictly unicellular organisms. Sometimes the individuals remain more or less united by a gelatinous matrix, and thus form irregular masses or filaments, but in such cases each cell is self-sufficient and there is no evidence of division of labor among such cells. Bacterial cells, like the cells of the Cyanophyceae, are without definite nuclei.

These tiny organisms are all about us, in the atmosphere, in the soil, in all water which has not been recently boiled or filtered through the finest filters, and particularly in sewage. Living bacteria are present on the surface of all the objects about us except those which have recently been heated to a high temperature or otherwise sterilized. They are abundant upon the surface of the human body, in the intestinal tract, and on all the mucous membranes. They are seldom found within the tissues of plants and animals except when the organisms are suffering from one of the numerous diseases which bacteria may cause.

These organisms are very small but they vary in size within rather wide limits. Among the smallest known bacteria is a rod-shaped form which is $\frac{1}{2}$ micron long and $\frac{1}{8}$ micron wide, but the average dimensions of the rod-shaped forms are probably about 2 microns by $\frac{1}{2}$ micron. (A micron, the unit of microscopic measurement, is 1/1000 of a millimeter or about 1/25000 of an inch.) There are three principal morphological types of bacteria: spheres, rods, and spirals. These are spoken of respectively as **cocci** (singular **coccus**), **bacilli** (singular **bacillus**), and **spirilla** (singular **spirillum**).

Some bacteria are able to swim about in a liquid medium by means of **cilia** or **flagella** (singular **flagellum**). These may arise from various parts of the surface of the cell.

The cell wall differs from that of typical plants in that it contains no cellulose. It is very similar chemically to the



FIG. 149.—Coccus forms of bacteria. A, *Staphylococcus*. B, *Diplococcus*. C, *Streptococcus*. D, *Sarcina*. All magnified about 1000 $\times$.

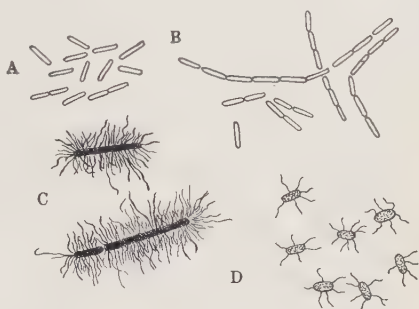


FIG. 150.—Bacillus forms of bacteria. A, *Bacillus sporogenes*. B, *Bacillus subtilis*. C, *Bacillus proteus*. D, *Bacillus typhosus*. All magnified about 750 $\times$.

protoplasm itself. The protoplast consists of cytoplasm through which are scattered particles of chromatin. That the protoplast is bounded by a semi-permeable membrane seems to be clear from the fact that the bacterial cell may be plasmolyzed. This fact is the basis of the commonly used methods of preserving food from spoiling by the use of salt or sugar, for when foods are preserved in sugar, sugar syrup, dry salt, or brine, the bacteria are unable to grow because of the withdrawal of most of their water by osmosis.



FIG. 151.—Spirillum forms of bacteria. A, a species of *Thiospirillum* (a sulphur oxidizing organism). B, *Spirillum undulm*. C, *Vibrio cholerae*. D, a species of *Spirochaete*. All magnified about 1000 $\times$.

Multiplication of Bacteria.—A bacterium which is abundantly supplied with food and surrounded by conditions favorable to it will grow to a certain maximum size and then divide by fission into two bacteria of equal size. Under favorable conditions the organisms increase in number by this method very rapidly, so that the descendants of a single bacterium may be within a few hours literally countless.

Spore Formation.—Some bacteria are capable of producing resistant spores. These structures can withstand high temperatures, the presence of poisonous substances, and other unfavorable conditions which are fatal to the ordinary vegetative cell. Fortunately, only a few disease-producing bacteria form spores. With few exceptions, the spores are produced singly within the ordinary bacterial cells. When these spores are formed the protoplast contracts, probably as the result of loss of water, and becomes surrounded by a relatively thick wall. Generally the wall of the cell within which the spore is formed is later dissolved away and thus the spore is freed. When temperature, moisture, food supply, and other conditions are favorable, the spores germinate, each giving rise to a single bacterium.

Since but one spore is produced within a vegetative cell and since each spore gives rise upon germination to a single bacterium, it is evident that spore formation is not a method of multiplication. The spores serve rather to tide the plant over periods which are unfavorable to vegetative activities.

Beneficial Activities of Bacteria.—Great as is the loss of life and property and the suffering for which some bacteria are responsible, the beneficial effects of bacteria doubtless outweigh the harm they do.

Their greatest single service is no doubt the part they play, together with the yeasts and molds, in causing the decay of plant and animal bodies. Through this process the carbon, oxygen, hydrogen, nitrogen, sulphur, and phosphorus which make up the bodies of animals and plants and their products are reduced to simple compounds, such as carbon dioxide, water,

nitrates, sulphates, and phosphates, which can again be used as raw material in food building by living plants. Were it not for this process of decay, in which bacteria play so important a part, much of the available supply of certain essential elements would remain permanently "locked up" in the dead bodies of organisms, so that what remained would not be sufficient for the growth and development of living plants and animals.

The fertility of agricultural soils is largely dependent upon the presence of soil bacteria, which not only make available certain of the essential elements already in the soil, but may increase the fertility of the soil by adding to the amount of nitrogen present in it. Bacteria are also essential to various industrial processes of great importance, such as butter and cheese making, and the preparation of vinegar.

Harmful Activities of Bacteria.—Bacteria are the causative agents in a large number of human diseases, including diphtheria, tuberculosis, anthrax, meningitis, typhoid fever, and many others. Most of the serious diseases of domestic animals are also bacterial. Whereas relatively few of the diseases of man and of animals are caused by any fungi except the bacteria, most of the diseases of plants are caused by higher fungi and relatively few by bacteria. Among the few bacterial diseases of plants are some very important ones such as the fire blight of pears.

Bacteria are also a source of serious loss to man because of the spoiling of food which is caused by them and by certain other fungi.

In addition to the soil bacteria which increase the fertility of agricultural soils, there are some which injure the soil by causing the loss of part of its combined nitrogen.

Fermentation.—Under the general term, **fermentation**, we shall include all those chemical changes involved in the breaking down by bacteria and by other fungi, of the proteins, carbohydrates, and fats of the bodies of plants and animals or of their products. The various bacteria of fermentation accomplish

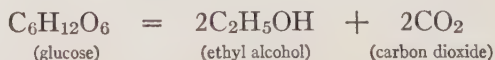
their characteristic chemical changes by the action of enzymes which they produce.

Different groups of bacteria are responsible for the fermentation of each of the three classes of foods, and no doubt often for different substances in each class. The bacteria concerned secure food for their own bodies from the substances fermented, and, from the decomposition of these fermented substances, the energy which they need for their own life processes.

Protein Fermentation.—The term **decay** is generally applied to the fermentation of proteins when it takes place in the presence of oxygen and when it is therefore not attended by offensive odors. When protein fermentation goes on under **anaerobic** conditions (in the absence of an abundant supply of oxygen), substances of offensive odor are produced and the process is spoken of as **putrefaction**. The products of protein fermentation, such as amino acids, may be further broken down by still other bacteria into such very simple substances as ammonia, nitrogen gas, hydrogen gas, carbon dioxide, hydrogen sulphide, methane (marsh gas) and water.

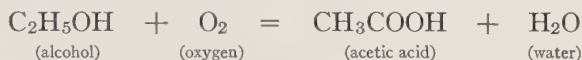
Fat Fermentation.—Relatively few bacterial forms are capable of fermenting fats, but a considerable number of other fungi may carry on this process.

Carbohydrate Fermentation.—The processes of carbohydrate fermentation are of great economic importance, one of the most important being **alcoholic fermentation**. Only a few bacteria are able to carry on this process, the most important agents being the yeasts, which are commonly classified among the Ascomycetes. By this process glucose and other similar sugars are transformed into ethyl alcohol and carbon dioxide.



After alcoholic fermentation has progressed to a certain point, the concentration of alcohol becomes sufficient to kill off the yeasts or at least to prevent their further activity. Then other

(acid) bacteria which were already present or which enter from the outside increase rapidly in number and bring about **acetic acid fermentation**. In this process the alcohol is converted into acetic acid and water.



Another type of carbohydrate fermentation, carried on principally by bacteria, is **lactic acid fermentation**, in which milk sugar (lactose) is changed into lactic acid. This occurs in the souring of milk.

Bacteria in Relation to Soil Fertility.—Of the essential elements secured by the green plant from the soil, nitrogen is, next to hydrogen and oxygen, the one which is needed in largest quantities. This element makes up a large part of the molecule of the different proteins of which protoplasm largely consists. Large quantities of the nitrogen from the soil which has been built into plant proteins of crop plants are removed from the field in the grain or other useful parts. Although the waste products from domestic animals, containing much of the nitrogen of the food which they have eaten and utilized in their metabolism, are in part returned to the soil as fertilizer, much of the nitrogen of the crops removed from the soil is never returned to it.

Nitrogen Fixation.—In the absence of all nitrogen except free nitrogen (nitrogen not combined with other elements) the higher plants do not thrive. Nitrogen in the form of nitrates (salts in which nitrogen and oxygen, in the proportion of one atom to three, are united with some metal, as in NaNO_3 , KNO_3 , and $\text{Ca}(\text{NO}_3)_2$) is the most favorable for the use of crop plants. Nitrogen in the form of ammonium salts (salts in which nitrogen and hydrogen are in the proportion of one atom to four, as in $(\text{NH}_4)_2\text{CO}_3$ and NH_4NO_3) can also be used but is less favorable. A number of agencies can cause the free or gaseous nitrogen of the atmosphere to unite with other elements and thus make it available for the use of green plants. — This union of

free (gaseous) nitrogen with some other element or elements to form a compound is called **nitrogen fixation**. The principal

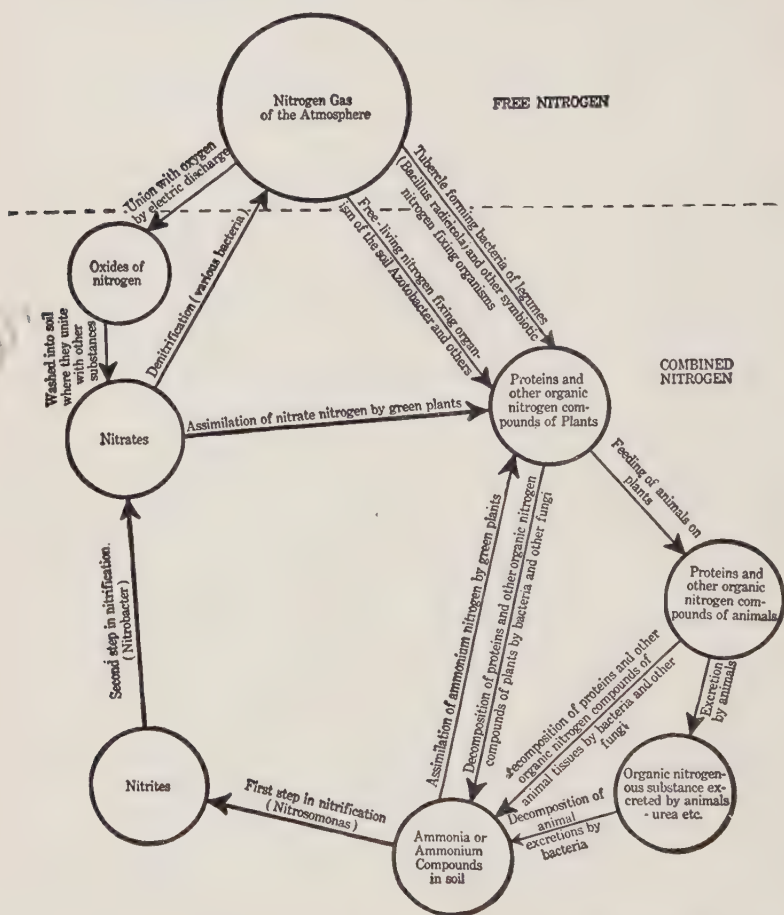


FIG. 152.—Nitrogen cycle diagram showing the principal changes in form which nitrogen may undergo in organisms.

processes by which nitrogen fixation takes place in nature are (1) electrical discharges in the atmosphere, (2) activity of bacteria living free in the soil, and (3) activity of bacteria living

symbiotically in the roots of certain plants. The quantity of fixed nitrogen which is added to the soil by the first of these processes is negligible.

The non-symbiotic nitrogen-fixing bacteria live free in the soil and have the power of combining the nitrogen of the air in the soil with other elements and thus building up the complex organic nitrogen compounds of their own cells. These complex compounds are later broken down by soil bacteria with the formation of nitrates. The best-known nitrogen-fixing bacteria living free in the soil are *Clostridium pasteurianum* and several species of *Azotobacter*.

In addition to the nitrogen-fixing bacteria which live free in the soil, there are others which live in the tissue of the roots of certain flowering plants, particularly members of the Leguminosae (bean family). The nitrogen-fixing bacterium which is commonly found in the roots of various beans, peas, lupines, clovers, and other leguminous plants is *Pseudomonas radiculicola*. There are, however, several different strains of this microorganism certain of which thrive only when associated with one or a few species of leguminous plants. These bacteria generally gain entrance to the roots when the latter are young through a root hair and by their presence cause the formation of swellings or tubercles upon the root. The cells of these tubercles are largely filled with bacteria. The atmospheric nitrogen is probably fixed by these organisms into organic nitrogen compounds. The plant bearing the tubercles is able to absorb and utilize this organic nitrogen or some simpler nitrogen compound arising from its partial decomposition. Leguminous plants growing in nitrogen-poor soil from which the proper strain of *Pseudomonas radiculicola* is lacking may be much stunted, but in the same soil in the presence of such bacteria they will thrive. Even after the removal of such a crop grown in association with the symbiotic nitrogen-fixing bacteria, the soil contains much more fixed nitrogen than before the infected legume crop was grown in it. The relation between *Pseudomonas radiculicola* and the leguminous

plant is certainly to be considered as one of **symbiosis** (living together of two kinds of organisms with mutual benefit). The bacteria secure food from the protoplasm of the leguminous plants in whose roots they live, and the legume secures nitrogenous compounds from the bacteria.

Nitrification.—Considerable ammonia is liberated in the soil as a result of the decay there of proteins from dead organisms or their organic products. If this remained in the form of ammonia gas it might diffuse into the atmosphere and thus be lost to the soil in which it was produced. Actually most of it is combined in the soil with other substances to form salts, such, for instance, as ammonium carbonate $(\text{NH}_4)_2\text{CO}_3$. Ammonium nitrogen is generally changed by bacteria in the soil into the nitrate nitrogen of such compounds as potassium nitrate and calcium nitrate (KNO_3 or $\text{Ca}(\text{NO}_3)_2$). This change is known as nitrification and is a process of great importance since nitrates are apparently a much better source of nitrogen for crop plants than are ammonium compounds. The transformation is known to take place in two stages: (1) the conversion of ammonium nitrogen into the nitrogen of nitrites, such as potassium nitrite, KNO_2 , and calcium nitrite, $\text{Ca}(\text{NO}_2)_2$; and (2) the conversion of nitrites into nitrates. The two stages are carried on by different bacteria. Several species of the genus *Nitrosomonas* are known to be able to bring about the first step and the second may be accomplished by bacteria belonging to the genus *Nitrobacter*. These two kinds of organisms always occur together and are common in soils and river water. As rapidly as nitrite is formed by *Nitrosomonas* it is converted into nitrate by *Nitrobacter*, so that in some cases it is not possible to detect nitrites in soils in which nitrification is going on. The nitrite and nitrate bacteria belong to a very small physiological group of bacteria which can exist in the absence of any organic material in the medium in which they grow. They are able to manufacture their own organic food out of carbon dioxide, water, and other simple inorganic substances. Thus they are very like inde-

pendent green plants as far as their independence of other organisms is concerned. They can make their own food, however, in the absence of light and in this respect are in striking contrast with green plants. The reason for this difference is that the nitrifying bacteria secure the energy for making their carbohydrates and other foods from the chemical energy liberated by the oxidation of ammonium nitrogen to nitrite nitrogen and of nitrite nitrogen to nitrate nitrogen. This process of food manufacture by the use of energy secured from a chemical change is called **chemosynthesis** as contrasted with photosynthesis.

Denitrification.—There have been found in soil and in manures as well as in the air and in natural bodies of water, bacteria which, instead of increasing the quantity of nitrate nitrogen, carry on the reverse process and convert nitrates into nitrites or gaseous oxides of nitrogen or even into free nitrogen. If this process of denitrification results in the formation of free nitrogen, the nitrogen passes into the air and is lost from the soil.

The Carbon Cycle and the Nitrogen Cycle.—As we have learned in earlier chapters autophytic plants build up the simple inorganic substances, water, carbon dioxide, and salts containing calcium, potassium, magnesium, iron, sulphur, nitrogen, and phosphorus into relatively complex organic substances which constitute the food not only of these green plants but also of all animals and heterophytic plants. These organic substances are broken down again in the destructive process, respiration, which goes on in all living organisms. In the dead bodies of plants and animals and in the excretions of animals there are large quantities of carbon, nitrogen, and the other essential elements (in the form of organic compounds) which are not available for the use of green plants. Various bacteria and other fungi can “unlock” the organic compounds of dead plants and animals and of the excretions of animals and convert the essential elements into forms in which they can be used again as raw material for food manufacture by autophytic plants.

Thus it is that these elements pass repeatedly through a cycle in which they are first converted from simple to complex compounds and then returned to the simple form by respiration or

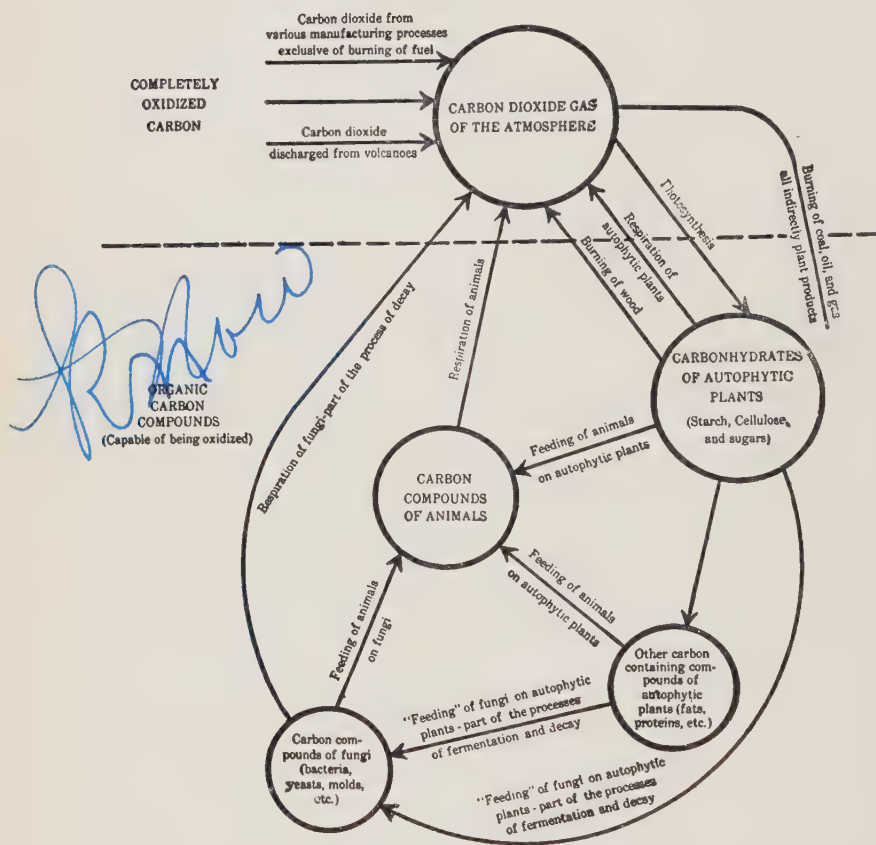


FIG. 153.—Carbon cycle diagram, showing the principal sources of the carbon dioxide of the atmosphere and the principal changes which carbon may undergo in organisms.

by fermentation by bacteria and other fungi. If we could trace the history of any nitrogen or carbon atom, for instance, we might find that it had been part of hundreds of different organ-

isms in succession; that it had literally "transmigrated" from an oak, to a bacterium, to a wheat plant, to a man, to a worm, and thus through innumerable changes throughout the ages since life first appeared upon the earth. The principal changes which carbon and nitrogen may undergo in one such cycle are graphically shown in the accompanying diagrams (Figs. 152 and 153).

MYXOMYCETES

Characteristics of the Myxomycetes.—In the Myxomycetes there seems to be a combination of animal and plant character-

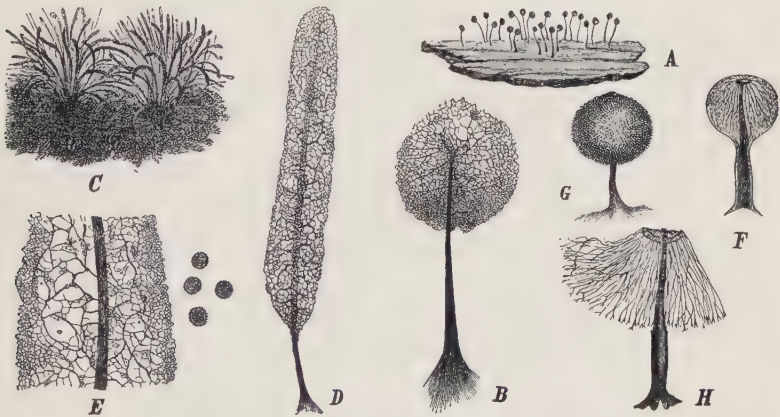


FIG. 154.—Myxomycetes. A-B. *Comatricha nigra*; A, group of sporangia, natural size; B, a single sporangium enlarged showing the stalk and the net-like capillitium. C-E, *Stemonitis fusca*; C, sporangia, natural size; D, a single sporangium enlarged showing the stalk and capillitium; E, portion of capillitium and spores. F-H, *Enerthema papillatum*; F, unripe sporangium; G, mature sporangium; H, capillitium. (C, D, after Harshberger. A, F, G, H, after Rostafinski; B, E, after de Bary; all from Harshberger's *Mycology and Plant Pathology*.)

istics, and on this account these organisms have excited the interest of both botanists and zoologists. During the vegetative part of their existence these plants consist of multinucleate masses of naked protoplasm, termed **plasmodia** (singular **plasmodium**), and are capable of **amoeboid** movement (movement

by flowing) of arm-like portions of the protoplasm, known as **pseudopodia**, and can flow around and engulf solid food particles. These characteristics—absence of cell walls, locomotion by streaming of protoplasm, and ability to take solid food particles into the protoplasm—are generally considered to be animal characteristics. In their reproduction, however, the Myxomycetes are more like certain plants (some kinds of fungi) than they are like any animals, and their spores have cellulose walls, another plant characteristic. With the exception of two or three parasitic genera, such as *Plasmodiophora* which causes the disease known as “Club Root” of cabbage and other crucifers, they are all saprophytes, securing their food from the decaying leaves and twigs and rotting wood of moist habitats, mostly in the forests. Because of their delicate structure and occasionally brilliant coloring, many of the Myxomycetes are of remarkable beauty.

PHYCOMYCETES

Characteristics.—This class of fungi is called the Phycomycetes (alga-like fungi) because of the close resemblance which they show to certain algae (1) in the structure of the filaments, **hyphae**, which make up the plant body, and (2) in their method of reproduction. The hyphae are like the filaments of some green algae, **coenocytic** tubes, that is, they have no cross walls except where the reproductive organs are cut off and accordingly the filaments are filled or lined with continuous multinucleate protoplasm. The absence of cross walls in the hyphae is characteristic, and by this vegetative feature alone they can usually be distinguished from the sac-fungi (Ascomycetes), and the basidium fungi (Basidiomycetes) both of which groups have **septate hyphae** (with cross walls separating uninucleate or multinucleate cells). The group includes both parasitic and saprophytic species.

There are two sub-classes of Phycomycetes, the Oomycetes, and the Zygomycetes. The Oomycetes are chiefly aquatic, or

at least at some portion of their life are dependent upon water for spore distribution, because of the development of motile asexual spores (zoospores), whereas the Zygomycetes are principally aerial and produce non-motile spores.

The Oomycetes are heterogamous, producing unlike gametes which unite to form an oospore. The Zygomycetes are isogamous, the gametes being similar and uniting to form a zygospore.

Representatives of the Phycomycetes.—*Saprolegnia* (Water Mold).—Most of the species of *Saprolegnia* (which belongs to the Oomycetes) are saprophytic on the bodies of dead insects and crustacea or on other decaying organic matter. A few species are parasitic and attack living fish or fish eggs, sometimes being very destructive when they infest the eggs and young fish in fish hatcheries.

The hyphae penetrate the substratum (material upon which they live), and absorb organic substances which they use as food and which make possible the growth of the organism. As in some of the algae, terminal portions of the hyphae become swollen and separated off by cross walls, and the contents divide into numerous uninucleate, biciliate zoospores. A peculiarity of *Saprolegnia* is that each one of these zoospores, instead of germinating to form new hyphae, comes to rest and forms a

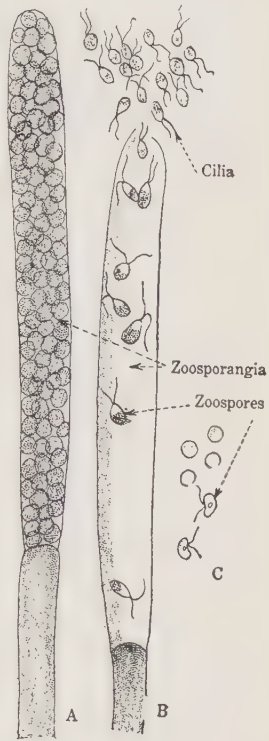


FIG. 155.—*Saprolegnia* showing asexual reproduction. A, a mature zoosporangium a short time before the liberation of the spores. B, a zoosporangium discharging zoospores which have terminal cilia. C, several of these zoospores which have become encysted; also two of the laterally biciliate zoospores which develop from the encysted zoospores.

wall, the protoplast then escaping and forming again a single biciliate zoospore, which in turn gives rise to new filaments. It is not clear what the significance of the two different zoospore stages is.

The sexual reproduction is heterogamous and very similar to that of certain green algae. The male gametes are not

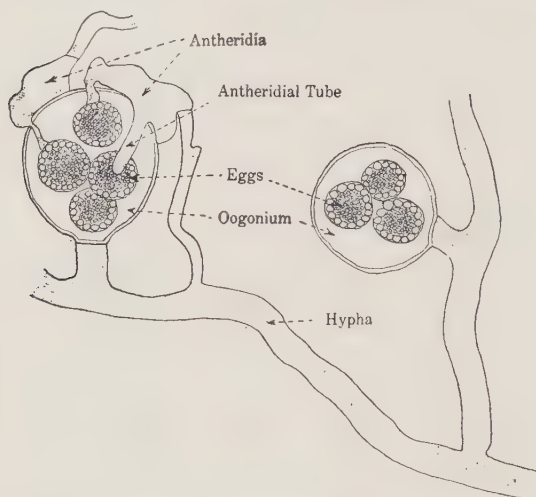


FIG. 156.—Sexual reproduction in *Saprolegnia*. (Redrawn from Sinnott in *Botany*, McGraw-Hill Book Co., Inc.)

ciliated and the oospores, upon germination, give rise directly to new hyphae.

Albugo candida is a parasitic representative of the Oomycetes which attacks members of the mustard family, causing a disease known as **white rust**. The **mycelium** (collective name for the vegetative hyphae of a fungus) occupies the intercellular spaces within the tissues of the host, and sends out small, slender, lateral projections called **haustoria**, which penetrate the cell walls, enter the cells, become swollen at the tips, and act as absorbing organs. Chains of asexual, multinucleate spores, known as **conidiospores**, are produced, under the epidermis of

the host, by constrictions of erect hyphal branches, which are called **conidiophores**. Each of these non-motile, multinucleate conidiospores breaks up into many motile zoospores which in

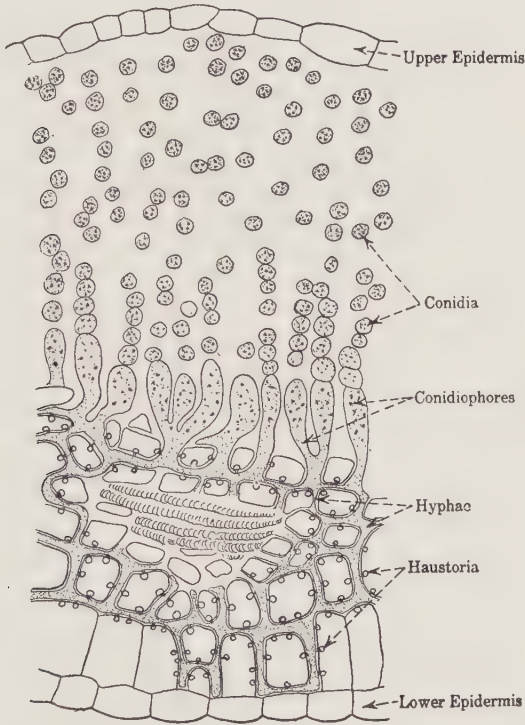


FIG. 157.—“White rust” of crucifers (*Albugo candida*) on shepherd’s purse, showing the hyphae with their knob-like haustoria, the erect conidiophores, and multinucleate conidiospores. Note that by growth of the conidiophores and conidiospores the epidermis is being torn from the underlying mesophyll. (Redrawn from Chamberlain.)

time germinate to form a new mycelium. Heterogamous sexual reproduction also occurs.

The common bread mold, *Rhizopus nigricans*, is the best-known representative of the Zygomycetes. It is very commonly found growing on stale bread, decaying fruit and vegetables,

and other organic materials left exposed to the air in moist places. *Rhizopus* spores are almost always present in the atmosphere except just after a heavy rain or snow storm when the air is almost free of bacteria and fungus spores. The mycelium consists of profusely branching coenocytic hyphae, which grow upon and within the substratum which supplies the

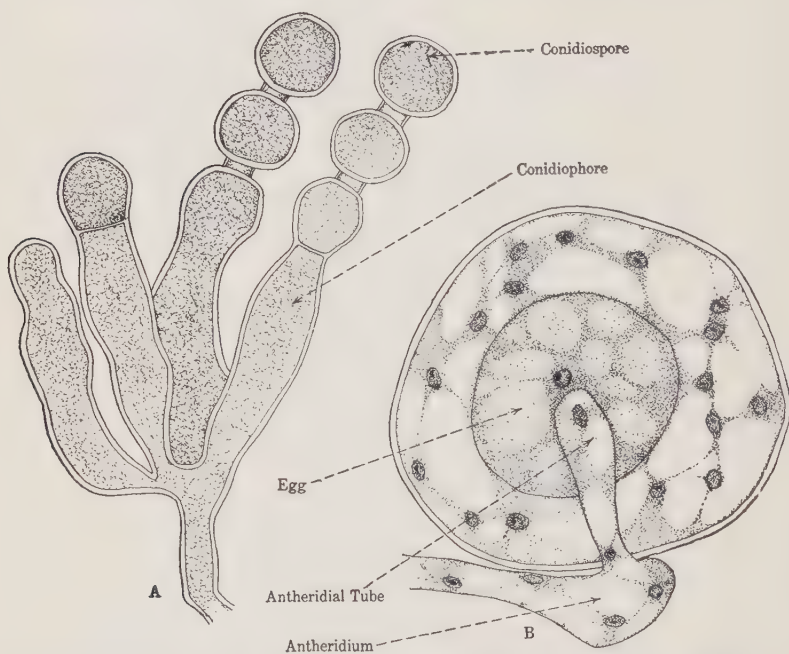


FIG. 158.—“White rust of crucifers” (*Albugo candida*). A, showing development of conidiospores. B, fertilization.

necessary foods. Certain hyphae, called **stolons**, of larger diameter than those which are formed within the substratum, grow just above its surface for a short distance, coming into contact with the substratum here and there along their length. At the points of contact there are produced clusters of hyphal branches which penetrate the material upon which the fungus

is growing and constitute holdfasts which somewhat suggest in their appearance the roots of higher plants (see Fig. 160). Later there arise at these points groups of erect branches, **sporangiophores**, upon which the **sporangia** (spore containing structures) are produced (Fig. 161). The spores are non-motile, multinucleate, and surrounded by a thick, black, cellulose wall. The method of their formation and release from the sporangium is shown by Figs. 160 and 161.

In sexual reproduction pairs of club-shaped hyphal branches are formed which come into contact at their tips (Fig. 162). The mass of dense protoplasm in the tip of each of these branches is cut off by a cross wall. The enclosed compartments thus formed are the **gametangia** (gamete-bearing organs), and the mass of multinucleate protoplasm enclosed in each is a **coenogamete**. Following dissolution of the walls of the gametangia at the point

of contact, the two adjoining coenogametes fuse, and, inasmuch as the two fusing masses are alike in structure, the fusion is spoken of as conjugation. The zygospore thus formed develops a thick, black wall about itself. After a resting period the zygospore may under favorable external conditions germinate and send out single sporangiophore, at the tip of which a sporangium containing asexual spores is formed. In *Rhizopus nigricans* conjugation does not take place between

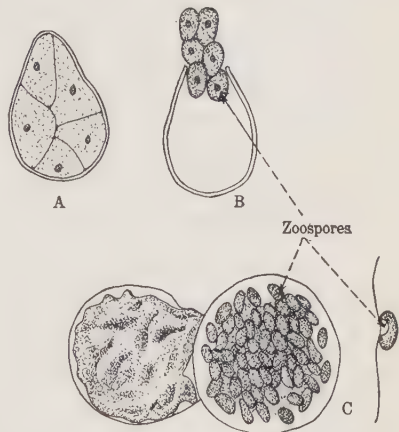


FIG. 159.—“White rust” of crucifers (*Albugo candida*). A, conidiospore, the protoplasmic contents of which have divided preparatory to zoospore formation. B, zoospores, with cilia not yet extended, escaping from conidiospore. C, germinating oospore discharging the numerous zoospores which for a time remain surrounded by a membrane. (C, redrawn from de Bary.)

any two hyphae which happen to be together. There are two strains or races of *Rhizopus nigricans*. These are designated as the "minus strain" and the "plus strain." Both strains must be present and the conjugation hyphae must be one of one strain, and one of the other, otherwise conjugation will not take place. Thus, there seems to be some physiological sexual differentiation although the gametes appear alike except for a slight difference in size. Sexual reproduction is not essential to the persistence of

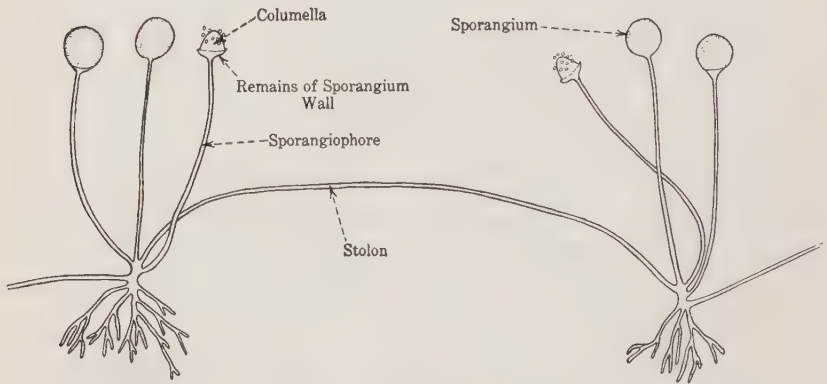


FIG. 160.—Bread mold (*Rhizopus nigricans*), showing groups of sporangiophores, rhizoid-like branches and stolons.

Rhizopus for the plant may propagate itself indefinitely by means of the asexual spores. There are many localities in which only one of the two strains of *Rhizopus* occur and although the mold may thrive in such regions, zygospores are never formed.

A group of parasitic fungi, known as the "downy mildews," also belongs to the Zygomycetes. These fungi cause serious diseases, such as the "late blight" of potatoes and the downy mildew of grapes and of other plants. The fungus spreads very rapidly by means of conidiospores, which are borne singly at the tips of branched conidiophores, and which may or may not form zoospores when they germinate.

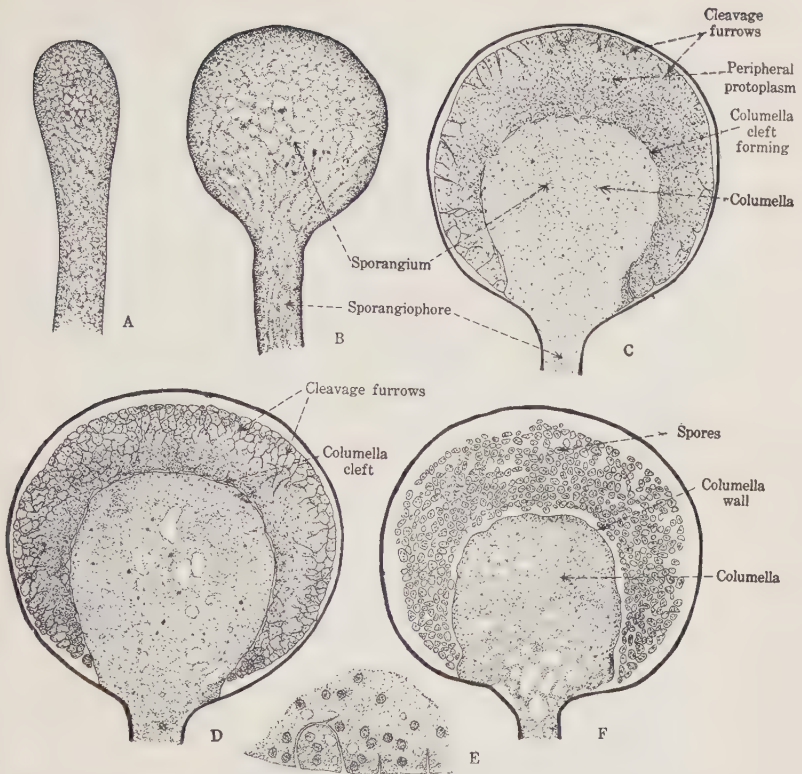


FIG. 161.—Stages in the development of the sporangia and in the formation of the spores of *Rhizopus nigricans* (common black mold) as seen in longitudinal sections. *A* and *B* show the enlargement of the free end of a sporangiophore to form the sporangium. *C*, *D* and *F* show the formation of the columella, and of the spores by furrowing of the protoplasm between the columella and the sporangium wall. *E* shows in greater detail a small portion of the cytoplasm of the sporangium represented in *C*. (Redrawn from D. B. Swingle's paper, Bureau of Plant Industry, Bulletin No. 37.)

ASCOMYCETES

Just **Characteristics of the Group.**—The Ascomycetes form the largest group of fungi and include a great variety of forms, many of which are of importance causal agents of various diseases of economic plants.

The one outstanding characteristic of the group, and the one that suggested the name of Ascomycetes, is the formation, either asexually or sexually, somewhere in the life history, of sac-like hyphae called **asci** (singular **ascus**) within each of which are produced a number of spores (generally eight), called **ascospores**. In addition to ascospores, conidiospores are also produced by many Ascomycetes. The hyphae of the Ascomycetes differ from

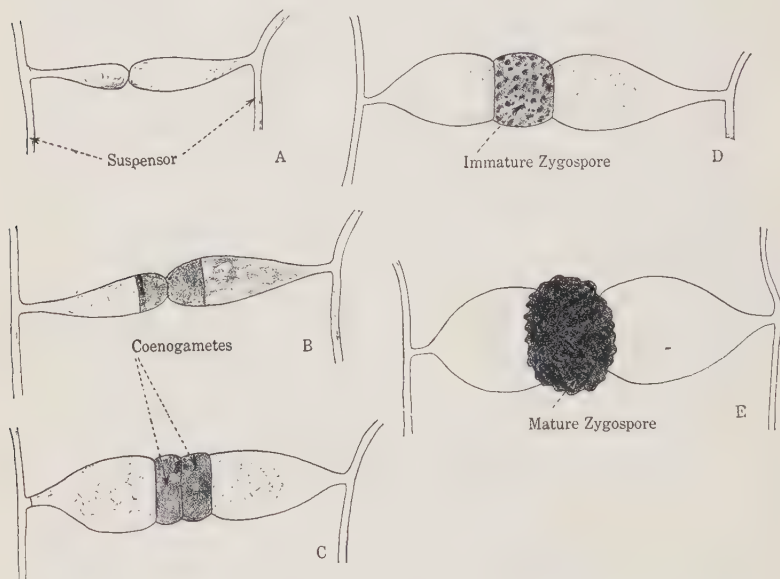


FIG. 162.—Bread mold (*Rhizopus nigricans*), showing stages in the formation of the zygospore.

the coenocytic hyphae of the Phycomycetes in being septate, that is, divided by transverse walls into cells, each of which may contain one or more nuclei.

In most Ascomycetes the asci are produced in special, often large and fleshy, fruiting bodies, called **ascocarps**. In *Peziza* and *Sclerotinia* the asci are borne in a cup-shaped or saucer-shaped ascocarp, which is called an **apothecium**. In the powdery mildews the asci are formed within a more or less spherical

ascocarp, called a **perithecium**, which is entirely closed. Thus ascocarps are either apothecia or perithecia.

There is a close similarity between certain Ascomycetes and certain of the Rhodophyceae as regards the structure of the gametangia and the behavior of the zygote. This likeness suggests a relationship between the two groups.

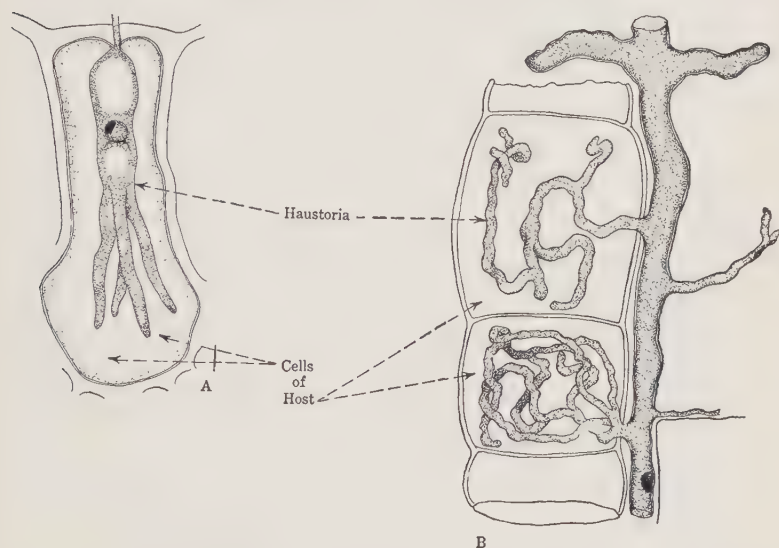


FIG. 163.—Haustoria of (A) a powdery mildew fungus (*Erysiphe graminis*) and (B) a downy mildew fungus (*Peronospora*). A redrawn from C. C. Curtis, B from Smith.

In addition to many important parasitic Ascomycetes causing plant diseases, the group also includes such non-parasitic forms of economic importance as the blue and green molds, so common on preserves and decaying fruit, the yeasts and the truffles.

Representatives of the Ascomycetes.—One of the most common saprophytic Ascomycetes is *Peziza*, which generally grows in soil very rich in organic matter or in decaying wood. There arises from the mycelium a conspicuous apothecium (open ascocarp) which is in the form of a cup and in some cases is brightly

colored within. In one species, *Peziza aurantiaca*, the inner surface of the cup is bright red. A section through the **hymenium** (tissue lining the interior of the cup) shows numerous cylindrical **asci**, each containing eight **ascospores**, and intermixed with the asci numerous sterile branches or hyphae known as **paraphyses**.

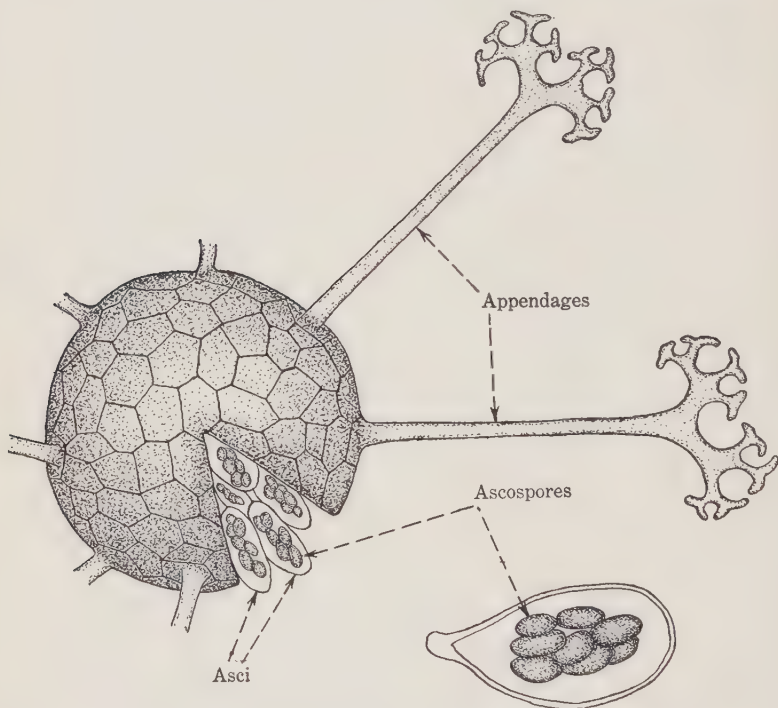


FIG. 164.—Powdery mildew of lilac, *Microsphaera alni*. Mature ascocarp, and at the right a single ascus.

The asci and paraphyses are perpendicular to the surface of the hymenium and parallel to each other.

No sexual reproduction has been found in *Peziza*, but it is known to occur in related forms. The union of a male and a female coenogamete results in a zygote which sends out a number of hyphae, at the tips of which the asci are developed. The

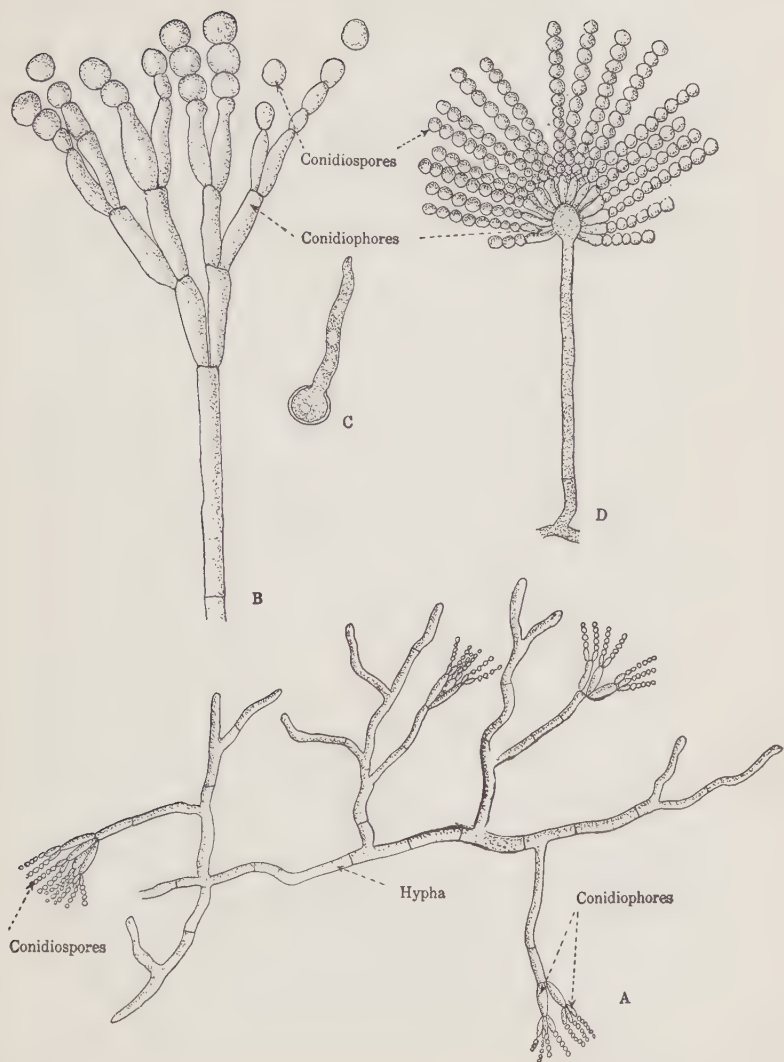


FIG. 165.—Blue and green molds. *A* and *B*, common blue mold (*Penicillium*). *C*, germinating conidiospore. *D*, green mold (*Aspergillus*).

paraphyses which are intermingled with the asci arise from beneath the oogonium. Other sterile hyphae form the cup-shaped ascocarp.

The “**powdery mildews**” constitute a large family of Ascomycetes all of which are strictly parasitic and produce their mycelium on the surface of the host. The hyphae bear **haustoria**, which penetrate the host cells. Asci are developed in perithecia (closed ascocarps), and the conidiospores which are produced in chains on the surface of the host, are often present in such immense numbers as to give a mealy or powdery appearance to the diseased structures.

The **blue** and **green molds** are well-known saprophytic Ascomycetes found on a great variety of substances. *Aspergillus* and *Penicillium* are the two most common genera. *Aspergillus* species occur on decaying vegetables of all sorts, on moldy cereals, on jellies, old leather, etc. The mycelium produced is prolific and spores arise in enormous numbers. Spores are developed on conidiophores, and arise by abstriction of terminal branches. The characteristic color of the mold appears when the conidiospores develop; in the different species they are various shades of green, brown, yellow, and red. The conidiospores, which are carried by air currents, and which when in abundance impart a characteristic moldy odor to the atmosphere, are capable of immediate germination if they fall upon the proper substratum.

Penicillium is the common blue mold on bread, cheese, lemons, etc. The conidiophores are branched, each branch bearing a chain of conidiospores. Sexual reproduction has been observed in several species of both *Aspergillus* and *Penicillium*.

The **yeasts**, some of which are of great economic importance, are usually included with the Ascomycetes because of their production, under certain conditions, of structures which somewhat resemble asci.

Yeast cells may remain attached in short chains but they do not produce a true mycelium. The cells are usually egg-shaped

or spherical and each cell is surrounded by a well-defined wall. Within the yeast cell may be discerned the nucleus, oil globules, and vacuoles. One of the chief characteristics of the yeasts is their method of vegetative reproduction by "budding." In this process a portion of the protoplasm of a cell surrounded by a cell wall forms a lateral outgrowth (bud) which outgrowth finally may separate from the parent cell and thus a new individual is produced.

Ascospores are produced only when there is an abundance of oxygen. In the production of ascospores the cell nucleus divides into several daughter nuclei, each one of which becomes the center of a spore lying within the original cell. The number of spores developed in a single yeast cell

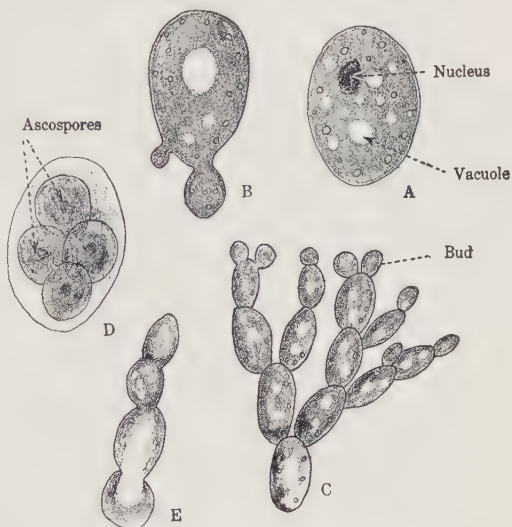


FIG. 166.—Yeast (*Saccharomyces cerevisiae*). *A*, single cell highly magnified. *B*, cell in process of budding. *C*, chain of cells formed as result of rapid budding and growth. *D*, formation of ascospores. *E*, germination of ascospore and the development of new plants by budding. (Redrawn from Curtis.)

varies, but it is usually four. On disintegration of the wall of the original cell, the spores are liberated, and under proper conditions produce new colonies of yeast plants.

The most important characteristic of the yeasts is their power of causing alcoholic fermentation. The yeast cells absorb certain sugars, and within the protoplast the sugar is decomposed with the formation of carbon dioxide and ethyl alcohol. (See page 234.)

This change is due to the presence in the yeast cells of the enzyme, **zymase**, which is a product of the protoplasm.

In this connection mention should be made of the remarkable group of plants known as the **lichens**. The lichens are of various forms and colors and are found in a great variety of situations. Some grow upon the soil, especially in far northern countries, others grow on the surface of rocks and old fences, and still others are epiphytes (organisms growing on the body of a plant but not living at its expense) on the trunks or branches of trees.



FIG. 167.—A crustaceous lichen.

The remarkable thing about the lichens is that the plant body is always made up of two different species growing together, one an alga, generally a green alga but sometimes a blue-green alga, and the other a fungus, generally an ascomycete. Neither

the fungus nor the alga if grown alone shows any resemblance to a lichen but when the algal species and the fungus species exist together in a relationship of symbiosis a characteristically formed and colored "compound organism" results which may be very successful in the struggle for existence even under conditions highly unfavorable to most plants.

Food is manufactured by the algal component of the lichen for its own use and for that of the fungus component as well. The fungus, on the other hand, probably serves the alga principally by absorbing and holding moisture. In addition to vegetative multiplication of the lichen the fungus can repro-

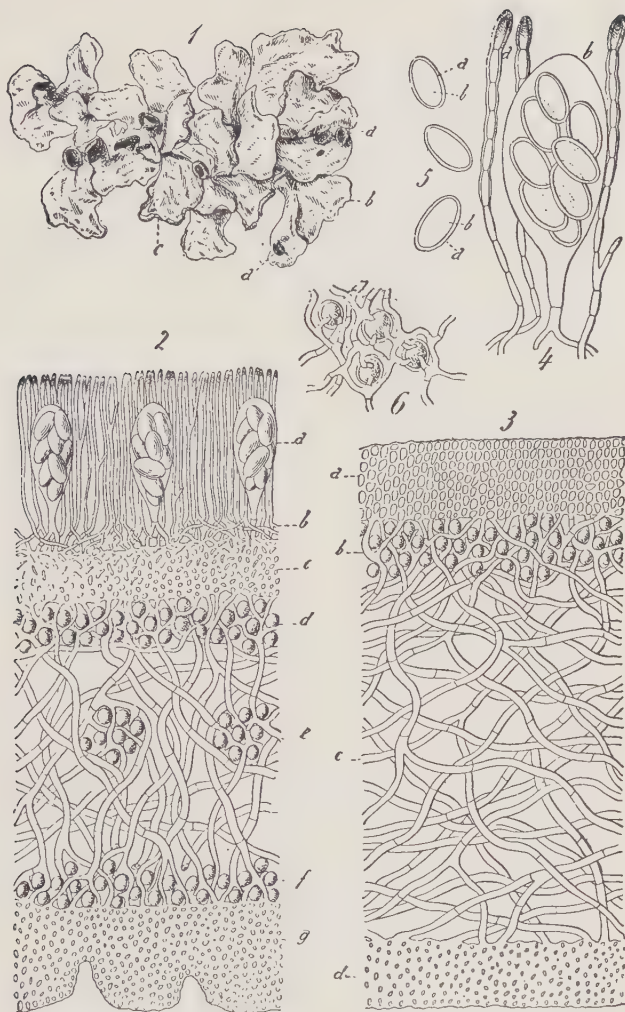
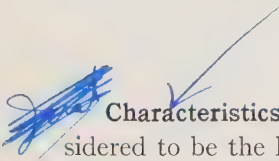


FIG. 168.—A lichen, *Parmelia perlata*. 1, Plant, slightly reduced; *a*, apothecia; *b*, lobe of thallus; *c*, soredia. 2, Longitudinal section of apothecium; *a*, asci and paraphyses; *b* and *c*, two layers of the hypothecium; *d*, upper algal layer; *e*, colonies of algae scattered among the hyphae; *f*, lower algal layer; *g*, lower cortical layer. 3, Cross section of vegetative portion of thallus. 4, Three paraphyses and a single ascocarp. 5, Ascospores. 6, Algal cell surrounded by fungal hyphae with haustoria. (After Schneider, from Gager.)

duce itself separately by the formation of ascospores. (See Fig. 168.)

BASIDIOMYCETES

 **Characteristics of the Group.**—The Basidiomycetes are considered to be the highest of the fungi, and to have been derived from the Ascomycetes. The group includes both parasitic and saprophytic species, many of which cause destructive plant diseases. The class name is descriptive of the outstanding character of the group, which is the occurrence of a special type of conidiophore, called a **basidium** (plural **basidia**), in the life cycle of these plants. It is a club-shaped hypha which produces non-motile asexual spores, **basidiospores**, singly at the ends of several (usually four) slender, pointed protuberances called **sterigmata** (singular **sterigma**). In some genera the basidium is divided by cross walls into a number of cells (generally four), but in other forms it is non-septate.

The hyphae which make up the mycelium are septate and branched. Gametangia have not been found, but there are simple nuclear fusions, however, which probably serve as fertilization processes.

Representatives of the Basidiomycetes.—*The Smuts.*—The most primitive of the Basidiomycetes are the **smuts**. All are parasites, occurring on a wide range of hosts, the most common hosts being the Gramineae, which include the grasses, and common cereals. The smuts are annually responsible for the loss of millions of dollars worth of corn, oats, barley, wheat, rye, and other cereals.

The smut of corn, *Ustilago maydis*, may be selected as a type form. The mycelium of the fungus may be found in any part of the host (Fig. 169), where it causes abnormalities and swellings, sometimes of considerable size. These "tumors" result from the abundant development of hyphae in the tissue of the host and further from the stimulation of the tissue of the affected

organ to abnormally active growth. Later, practically all of the internal tissue of the diseased part of the host is used up by the growth of the smut hyphae, so that the whole deformed structure, except the surface layers, becomes a mass of fungal hyphae. These hyphae are then transformed into millions of black spores known as **chlamydospores**. Each of these spores is formed from a short segment of a hypha which becomes surrounded by a slightly thickened wall and then separates from the adjoining segments of the same hypha. Chlamydospores are capable of germination as soon as mature if conditions are favorable, or they may retain their vitality throughout the winter and germinate the next spring. Each germinating chlamydospore produces a short hypha, called a **promycelium** or **basidium**, which is divided by cross walls into three or four cells. Each of these cells bears a single basidiospore which is generally spoken of as a **sporidium**. The sporidia are capable of saprophytic

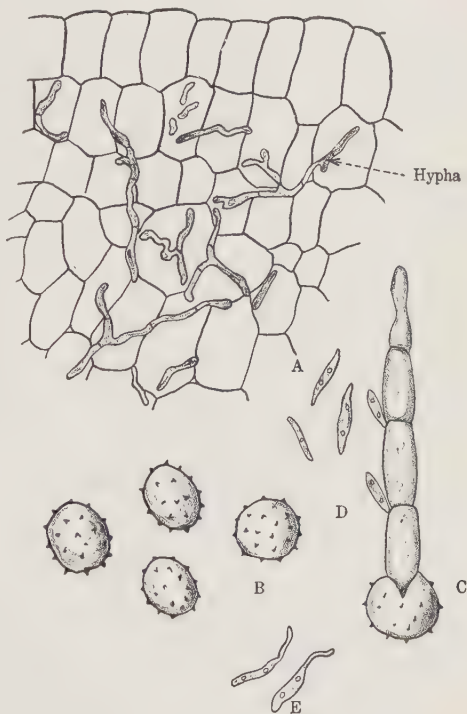


FIG. 169.—Corn smut (*Ustilago maydis*). *A*, hyphae in the tissue of the host. *B*, mature chlamydospores. *C*, a germinating chlamydospore, showing the 4-celled promycelium, two cells of which are producing sporidia (basidiospores). *D*, sporidia. *E*, budding sporidia. (Redrawn from Freeman and Stakman, in Minnesota Agricultural Experiment Station Bulletin.)

growth and multiplication by budding when appropriate organic matter is available. Such budding often goes on rapidly in barnyard manure. The sporidia are readily carried by the wind

and may, if they fall upon any young tissue of a corn plant, send out short hyphae which may penetrate the epidermal cells and thus infect the plant.

In some species of smuts the chlamydospores adhere to the surface of the seeds and infection takes place in the seedlings which develop from the germinating seeds (bunt of wheat and oat smut). In other species infection takes place through the ovary of the flowers so that the fungus hyphae are present in the embryos of the seeds when they ripen (loose smuts of wheat and barley). The proper treatment to reduce crop losses depends very largely upon what type of infection (seedling infection, flower infection, or general infection, as in corn) is characteristic of the particular smut species in question.



FIG. 170.—Wheat heads affected by bunt or stinking smut of wheat which is caused by *Tilletia*. The kernels alone are affected, each kernel being transformed into smut balls, which are rather compact masses of spores. (After Leach, in Colorado Agricultural Experiment Station Bulletin.)

The Rusts.—The rusts constitute another group of the Basidiomycetes which is of great economic importance. They are parasites on a great variety of hosts, chiefly seed plants.

The mycelium is composed of septate hyphae which nearly always grow in the intercellular spaces of the host tissue and are branched and provided with haustoria. Spores are usually produced in



FIG. 171.—Smutted oats. At the left, head affected by loose smut (*Ustilago avenae*); at the right, head affected by closed smut (*Ustilago levis*). (From Colorado Agricultural College Extension Service Bulletin.)

patches, called **sori** (singular **sorus**), on the surface of the host. Five different types of spores may be formed in rust fungi, but all are not present in every species.

One of the best-known genera among the rusts is *Puccinia*.

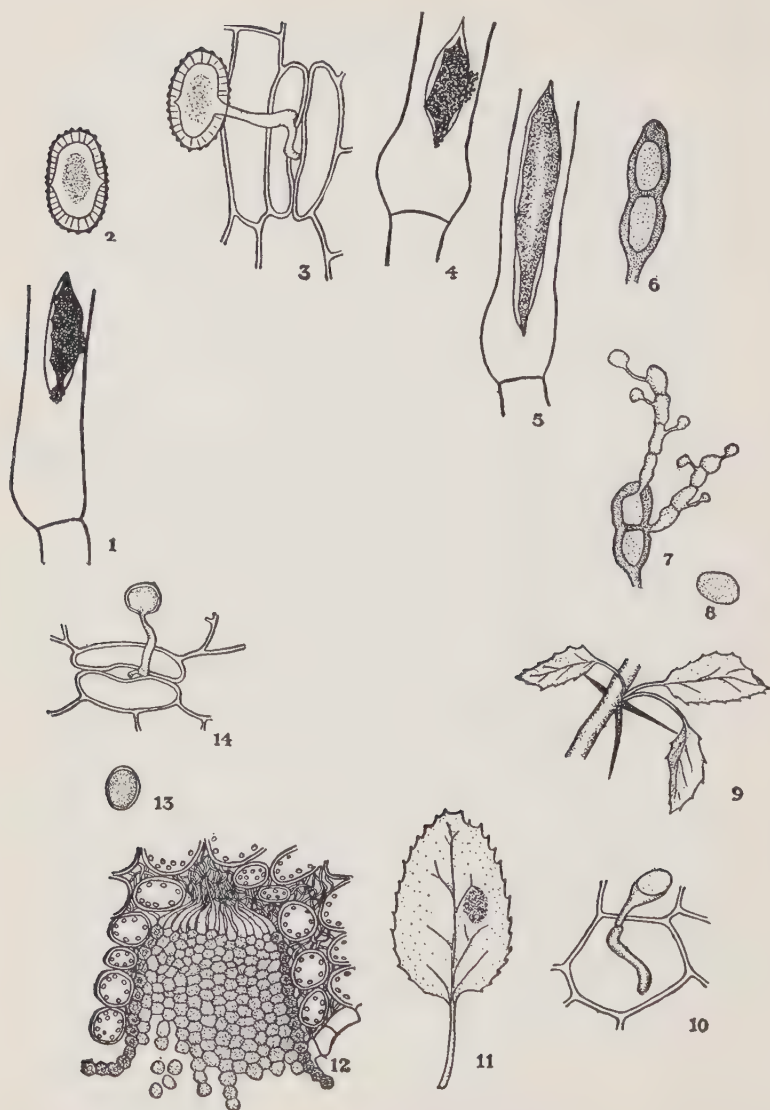


FIG. 172.—Life cycle of black stem rust (*Puccinia graminis*)—a heteroecious rust. 1, Uredosorus on wheat stem. The red uredospores which are produced early in the season are known as summer spores. 2, A single uredospore. 3, Germinating

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It has a number of economically very important species, chief of which is *Puccinia graminis*, the black stem rust of wheat, oats, barley, rye, and many grasses. The grain losses due to this parasite are sometimes enormous.

Most parasitic fungi require but a single host in order to complete their life cycle, but a few have two different host species and cannot complete their life cycle unless both are present. *Puccinia graminis* is one of the latter, requiring a grass host, such as wheat, as one host and the barberry as the second, or alternate host.

The first visible evidence of this rust on cereals is seen on stems and leaves as reddish-brown streaks or pustules, which make their appearance in the spring and summer. They are caused by groups (sori) of minute yellowish spores formed just beneath the epidermis of the host. These spores are known as **uredospores** (Fig. 172, 2), and the sori as **uredosori** (Fig. 172, 1 and 4). These spores give external evidence of the presence of a mycelium growing among the cells of the tissues of the host. The production of uredospores is spoken of as the "red rust"

uredospore on surface of the stem of another wheat plant, its germ tube penetrating a stoma. As a result a mycelium is formed within the tissues of the host and soon another crop of uredospores is borne in uredosori as shown in (4). Thus during a single season there may be many successive crops of uredospores, the disease spreading rapidly over a field. 5, A teleutosorus produced later on wheat stems. The dark teleutospores which are liberated from the sorus are known as winter spores. They remain alive on the straw during the winter. 6, A single teleutospore. 7, A teleutospore germinating, the spring following its formation. Both cells are sending out 4-celled promycelia (basidia) each cell of which may produce one sporidium (basidiospore). 8, A single sporidium. If the sporidia fall upon a common barberry leaf (9), they germinate as shown in (10), and the germ tube penetrates the leaf epidermis and forms a mycelium within the tissue of the leaf. 11, A barberry leaf (lower surface) showing a group of aecidia (cluster cups). 12, Section of an aecidium on lower surface of barberry leaf. This is filled with chains of yellowish one-celled spores (aecidiospores). 13, A single aecidiospore. 14, An aecidiospore germinating on the surface of wheat, the germ tube penetrating a stoma. The parasite spreads within the tissue of the host and after a time uredospores are produced in characteristic pustules or sori as shown in (1). (Adapted from figure in a Bulletin of the Minnesota Experiment Station.)

stage of the disease. Each uredospore is stalked, one-celled and generally oval in form, and has a rather thick wall which bears numerous short spiny projections. These spores are dis-

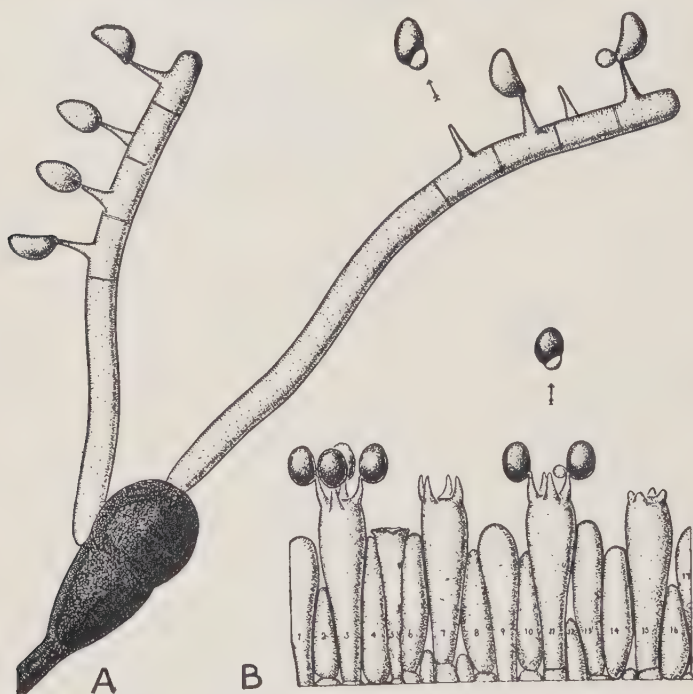


FIG. 173.—Basidiospore-discharge in the Uredineae and the Hymenomycetes. *A*, a germinated teleutospore of *Puccinia graminis* (from *Avena sativa*) bearing two basidia, one with four ripe spores still attached and the other with spore-discharge taking place. *B*, a transverse section through the hymenium of *Psalliotia campestris*, showing a basidium with four ripe spores and another basidium with spore-discharge going on. In both *Puccinia graminis* and *Psalliotia campestris* a drop of water is excreted from the hilum of each spore just before discharge. Magnification the same both *A* and *B*, 880. (From Buller's *Researches on Fungi*.)

seminated by the wind. They are capable of germination within four or five days after they are shed, if sufficient moisture is present. Infection takes place by the growth of the germ tube through a stoma into the host tissue. Within the host tissues

this hypha branches and forms a new mycelial growth. Within a short time the mycelium absorbs sufficient food from the host to form a new crop of uredospores. Thus it is possible to have a considerable number of successive crops of uredospores in a single season, and from one or a few infected plants the disease may spread over a large field.

Usually in the late summer or fall when the grain begins to ripen, black pustules or sori appear on the same stems and leaves which produced the uredosori. These black sori consist of dark-colored spores known as **teleutospores**. (See Fig. 172, 5 and 6.) The sori are called **teleutosori**. The teleutospores are stalked, two-celled structures, which are spindle-shaped and have a thick wall. They are unable to germinate at once as do the uredospores, but after wintering in the open on stubble or on the soil, they germinate freely.

At germination one or both cells of the teleutospore may send out a tube, which, as in the smuts, is called a promycelium or basidium (Figs. 172, 7 and 173A). This is generally a four-celled structure, each cell of which forms a single colorless sporidium, **basidiospore**, on a short **sterigma**. The basidiospores are carried by the wind. They will not germinate and bring about infection unless they fall upon the leaves, twigs, or fruit of certain species of barberry, the most important of which is the common barberry (*Berberis vulgaris*). Here a germ tube is formed which penetrates the tissues of the plant, entering through a stoma.



FIG. 174.—Leaf of common barberry (*Berberis vulgaris*), showing clusters of aecidia (cluster cups) on the lower surface. (From Buller's *Researches on Fungi*.)

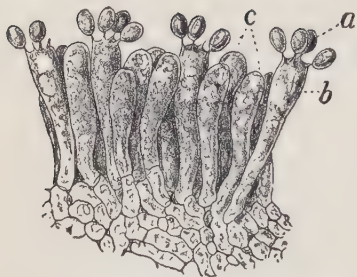


FIG. 175.—Small portion of a section through the spore-bearing layer (hymenium) of a mushroom. *a*, basidiospores; *b*, a basidium; *c*, paraphyses. (After Longyear, in Colorado Agricultural Experiment Station Bulletin.)

Within seven to ten days after the barberry plants are infected by basidiospores there appear, submerged below the surface on the upper side of the leaves, small flask-shaped bodies which break through the epidermis. Somewhat later, clusters of yellowish cups are found on the lower surface of the leaf.

The small flask-shaped bodies are known as **spermagonia**. Within them are produced rod-shaped or oval **spermata**. These latter bodies apparently do not

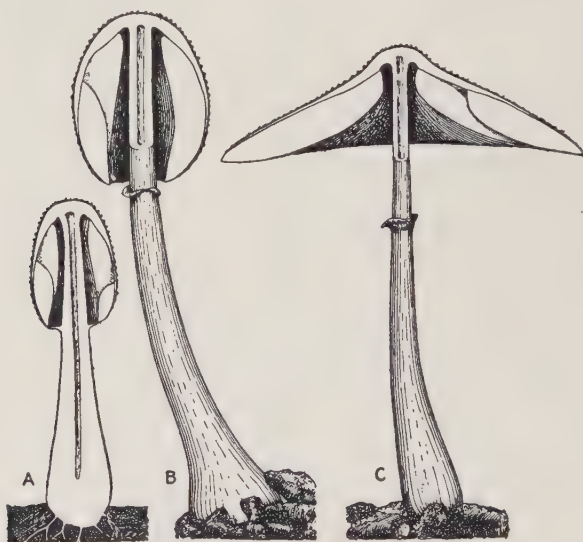


FIG. 176.—*Lepiota cepasestipes*. Sections of three fruit-bodies coming up among cinders, Sphagnum, etc., in a hothouse. *A*, in the morning, the gill-chamber still intact. *B*, in the afternoon, the pileus beginning to expand, an annulus left upon the stipe. *C*, at night, the pileus fully expanded and shedding spores. Natural size. (From Buller's *Researches on Fungi*.)

function in the life history of the fungus. The cup-shaped structures are called **cluster-cups** or **aecidia** (Fig. 172, 11, 12, and 13 and 174). At maturity these are filled with chains of yellowish one celled spores, known as **aecidiospores**. The aecidiospores



FIG. 177.—Under surface of fruit-body of *Polyporus squamosus* nearly full grown, showing the pores of the hymenial tubes and the reticulations on the stipe. The fruit-body was photographed immediately after it was cut; the involution of the edge of the pileus is quite natural. Photographed by R. H. Pickard. One-third natural size. (From Buller's *Research on Fungi*.)

are scattered by the wind and may infect the grass host. A mycelium is developed within the tissues of the grass plant, and gives rise to uredospores in the manner already described.

~~The~~ **Fleshy and Woody Basidiomycetes.**—The most familiar representatives of the Basidiomycetes are the fleshy and woody

forms such as the mushrooms, puff balls, and the bracket fungi which are often found on trees. A characteristic feature of these forms is the conspicuous spore-producing part which in some cases may attain considerable size and which produces the hymenium, a compact layer consisting of one-celled basidia, each bearing basidiospores, generally four to a basidium.

The mushroom, as we ordinarily know it, is not the whole plant but merely a reproductive structure or sporophore. The



FIG. 178.—A cluster of puff-balls (*Lycoperdon*). (After Longyear.)

vegetative part of the plant body is the mycelium, which grows saprophytically in soil rich in organic matter or other substratum upon which the sporophores are produced. It consists of extensively branched strands of hyphae which absorb and use as food organic material in the substratum. On this account mushrooms are never found except in locations where there is an abundance of organic material, such as decayed leaves and twigs, or manure. It is only after the mycelium has accumulated considerable stores of food that the sporophores are produced.

The mature sporophore, or fruiting body, consists of a stalk.

or **stipe** and an umbrella-shaped cap called the **pileus** (Fig. 176). On the under side of this cap there are borne thin plates called **gills** which radiate from the stalk toward the margin of the pileus and are covered by hymenium. This surface layer of the hymenium is made up of millions of basidia and sterile hyphae or paraphyses growing out at right angles to the surface of the gill. (See Figs. 173 *B* and 175.)

Basidiospores are produced in immense numbers on the hymenium, up to 1800 million by a single sporophore of the common field mushroom. The mushroom (*Agaricus campestris*) is a purple-spored form, whereas the genus, *Amanita*, which includes many poisonous species of gill fungi, is characterized by having white spores. The spores drop from the sterigmata of the basidia upon which they are borne, and are readily carried far and wide by air currents. Under favorable conditions they germinate and develop new mycelium.

In the bracket fungi (Fig. 177) the hymenium forms the lining surface of many pores formed on the lower side of the sporophores.

CHAPTER XII

BRYOPHYTA (LIVERWORTS AND MOSSES)

CHARACTERISTICS OF THE DIVISION

THE algae, which are the ancestors of the mosses and liverworts, are, with few exceptions, aquatic plants. The mosses and liverworts, on the other hand, are the most primitive of the truly terrestrial or land plants, although their adaptation to land conditions is so imperfect that few of them, if any, are able to complete their life cycle without being subjected to a period during which the plant is actually covered with water.

The adoption of a land habitat by the Bryophyta and higher land plants has necessitated certain structural and physiological adaptations in response to the great difference in the environment of land plants and that of submerged aquatics.

Some of the principal characteristics of the Bryophyta and of higher land plants which are apparently correlated with the differences in environment are:

- (a) Special structures for the absorption of water and minerals from the soil are developed by all typical land plants—the **rhizoids** of lower land plants (Bryophyta) and the roots and root hairs of ferns and flowering plants. The rhizoids of the Bryophyta appear, however, not to be very efficient organs for water absorption.
- (b) The parts exposed to the air are protected from excessive water loss by the production of a superficial layer of cells (epidermis) having an outer wall which, with its

cuticle, is very resistant to the passage of water vapor. It is important that this should not prevent the entrance of the gases needed for photosynthesis and respiration. The epidermis among most land plants, accordingly, has openings through it, called stomata.

- (c) In all but the smallest land plants there are conductive tissues which provide for the relatively rapid transfer of water from the water-absorbing structures to the parts exposed to the dry atmosphere.
- (d) The more primitive land plants either grow prone upon the ground or, if erect, seldom attain a height of more than a centimeter or two, since they are lacking in mechanical tissues. The higher land plants have developed mechanical tissues and some of them are able to support a stem hundreds of feet high.
- (c) In the Bryophyta, and in the Pteridophyta as well, fertilization can take place only when the plants which bear the gametes are wet, because the sperms can move only in water. By various means the spores of land plants are adapted to efficient dissemination by air instead of water. Small size and the development of ridges or spines on the outer spore wall are among the principal characteristics favoring wind dissemination. The discharge of spores into the air from elevated structures, such as the long-stalked capsules of the mosses and many liverworts, makes it more likely that they will be carried to some distance by air currents before they fall to the ground.

CHARACTERISTICS OF THE BRYOPHYTA

The single most important point of distinction between the Bryophyta and the Algae is the alternation, in the life cycle of all the Bryophytes of a sexual generation and an asexual generation. This alternation of generations occurs in a few of the Thallophyta but is not characteristic of the group. The asexual

or spore-bearing plant is known as the **sporophyte**, and the sexual or gamete-bearing plant is the **gametophyte**.

In all the Bryophyta the gametophyte is "the plant," that is to say, the gametophyte is the conspicuous and independent plant, which alone is able to absorb water and soil solutes and to which the function of food manufacture is entirely or largely restricted. The sporophyte is smaller than the gametophyte and is permanently attached to and grows more or less parasitically upon the gametophyte, never establishing direct connections with the soil. It is among the Bryophyta that the gametophyte reaches its highest development among plants. The gametophyte at its best, however, never becomes an efficient land plant.

Sexual reproduction is heterogamous, as in all plants above the Thallophytes. The female gametangium, called the **archegonium** in the Bryophyta and Pteridophyta, does not consist of a single cell, the protoplasm of which forms one or several female gametes (egg cells) as does the oogonium of the Thallophyta. Instead it is a **multicellular** flask-shaped **organ**, and the single egg cell is surrounded by a wall made up of **many cells**, instead of being surrounded by a **cell wall only** as in the Thallophytes.

The male gametangia or antheridia of the Bryophyta are also distinctly different from those of the Thallophyta, the wall surrounding the sperms produced by one antheridium being made up of a **layer of cells** instead of consisting, as in the Thallophyta, merely of a **cell wall**. This applies as well to the Pteridophyta as to the Bryophyta.

Fertilization cannot take place unless the plants are wet, for it must be possible for the sperms, which are ciliated protoplasts, to swim to the archegonia.

The asexual spores of the Bryophyta (and the Pteridophyta and Spermatophyta as well) are formed in groups of four (**tetrads**), each tetrad being formed as the result of two divisions of a single cell (the spore mother cell).

No true roots are formed in this division of the plant kingdom, but the sexual or gametophyte plants produce organs called

rhizoids which perform the functions carried on by the roots of ferns and seed-bearing plants.

The forms which are to be described in this chapter do not represent successive stages in evolution. They do, however, illustrate in all probability some of the principal steps which took place in the evolution of the sporophyte.

The Bryophyta are divided into two classes, the Hepaticae or liverworts and the Musci or mosses.



THE HEPATICAE (LIVERWORTS)

The members of this class are in general more strictly confined to very moist habitats than are the *Musci*. There are some species, however, which are able to survive months of almost complete desiccation. The sporophytes of the liverworts are less complex than are those of the mosses and for the most part somewhat smaller.

Representatives of the Liverworts.—*Riccia* is a type which illustrates the simplest sporophyte found in the liverworts, although the gametophyte is not so simple as are those of some other members of this class.

The gametophyte consists of a small, flattened, freely-branching thallus, with a depression along the middle line of the upper side (Figs. 179 and 180). From the under side of the thallus numerous rhizoids grow out. These are very similar to root hairs and are merely tubular extensions of certain of the cells of the lower surface of the thallus. They function as organs of attachment and absorption. The thallus consists of chlorophyll-bearing tissue above where food manufacture is carried on, and in the lower portion of colorless tissue which serves for food and water storage.



FIG. 179.—Thallus of a terrestrial species of *Riccia*. (Magnified about 8×.)

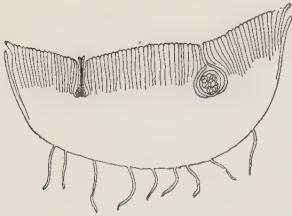


FIG. 180.—Cross section, somewhat diagrammatic, of the thallus (gametophyte) of *Riccia* showing on the left an unfertilized archegonium sunk in a deep depression. On the right is a sporophyte within the enlarged venter of an archegonium from the fertilized egg cell of which the sporophyte developed. The chlorophyll bearing tissue of the upper portion of the thallus is also shown as well as the colorless tissue of the lower part of the thallus, and the rhizoids. (Magnification about $30\times$.)

of the cavity of the venter. When the plants are wet the mature antheridia open as the result of the absorption of water by the gelatinous cell walls and their consequent swelling. The motile sperms are thus freed and swim to the opening of the neck of the archegonia, the neck cells of which have degenerated into a mucilaginous material and dissolved, leaving a free passage to the egg cell.

The formation of the zygote by the fusion of one sperm with each egg cell marks the beginning of the sporophyte or asexual gen-

The antheridia and archegonia (Figs. 181 and 182) are sunk in depressions in the thallus, opening out into the median furrow. In *Riccia* antheridia and archegonia are borne on the same thallus, but in many species of liverworts they occur on different plants. The biciliate sperms are formed in great numbers in pear-shaped antheridia each of which consists of a single layer of sterile cells enclosing the sperm cells. The archegonium consists of an enlarged basal portion, the **venter**, and a slender elongated tubular portion called the **neck**. The cavity of the neck and venter contains a single row of cells, the lowest one, which is the egg cell or female gamete, being the largest and occupying most

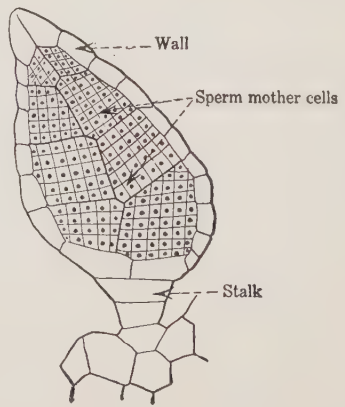


FIG. 181.—An antheridium of *Riccia* in section.

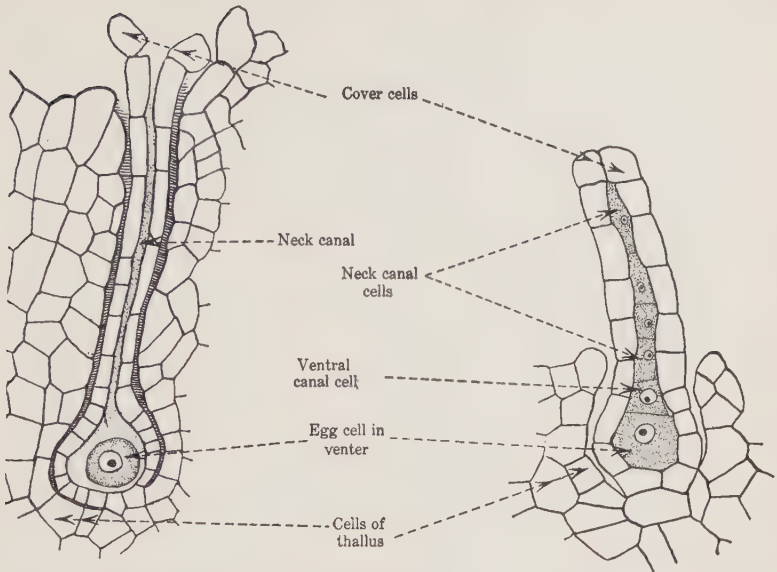


FIG. 182.—Archegonia of *Riccia* surrounded by the tissue of the thallus. To the right, an almost mature archegonium. To the left, an archegonium ready for fertilization. (Drawn from preparations of D. H. Campbell.)

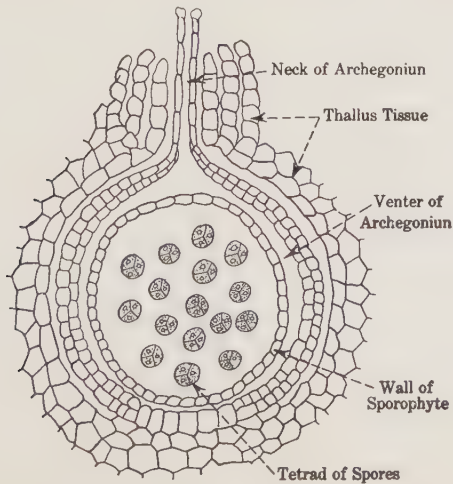


FIG. 183.—Diagrammatic figure showing, in a section cut at right angles to the surface of the thallus, the mature sporophyte and enlarged archegonium of *Riccia*.

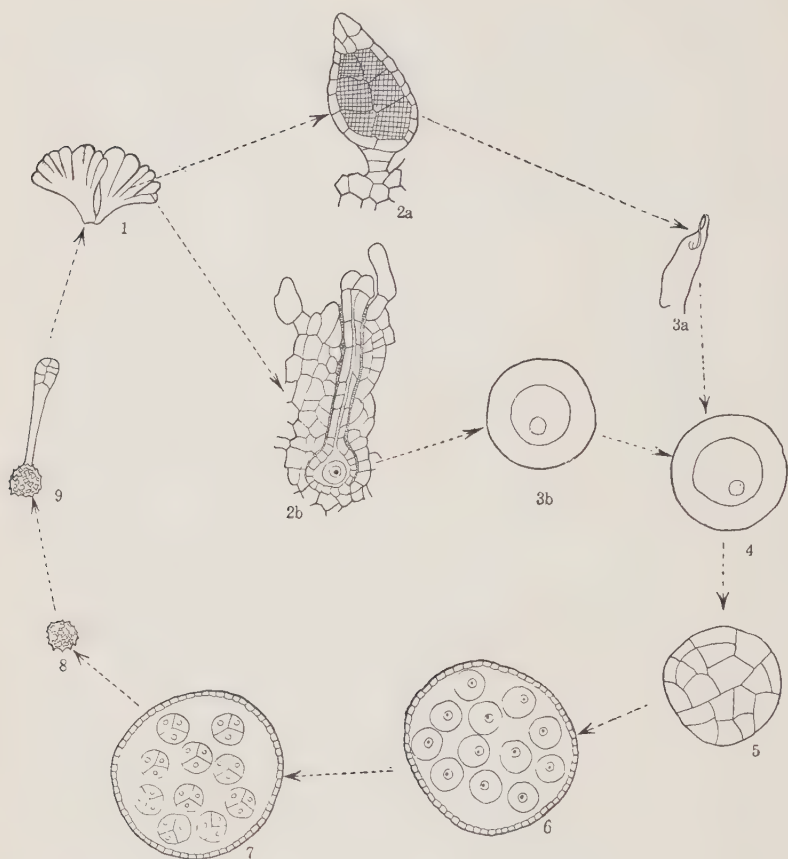


FIG. 184.—Diagram showing the life cycle of *Riccia*. 1, the gametophyte thallus (monoecious). 2a, antheridium. 2b, an archegonium ready to open and permit the entrance of sperms (both antheridia and archegonia are sunk in the tissue of the thallus). 3a, a single sperm. 3b, an egg cell. 4, the fertilized egg cell or zygote. 5, an embryo sporophyte resulting from repeated divisions of the zygote. 6, the sporophyte with contained spore mother cells. 7, tetrads of spores each such group of four resulting from two divisions (the first a reduction division) of a spore mother cell. 8, a single ripe spore. 9, a very young gametophyte plant developed from a spore. Note that stages 4–6 and the wall cells in 7 belong to the sporophyte generation, the other structures to the gametophyte.

eration. The sperm and egg cell and all the other gametophyte cells have the haploid (x) number of chromosomes but all the cells of this generation have the diploid chromosome number. The zygote, by repeated divisions, gives rise to a spherical structure (the sporophyte) many times the size of the zygote (Fig. 183). This structure consists of a wall made

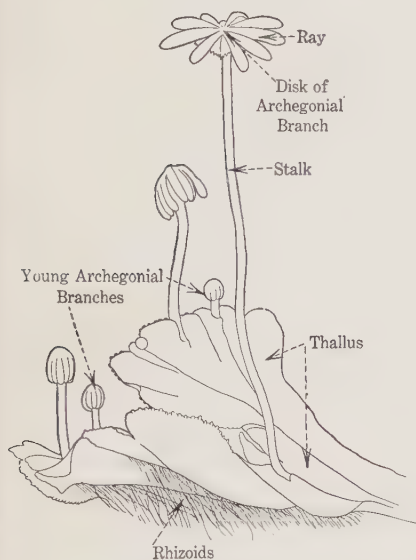


FIG. 185.—A portion of the female gametophyte of *Marchantia*.

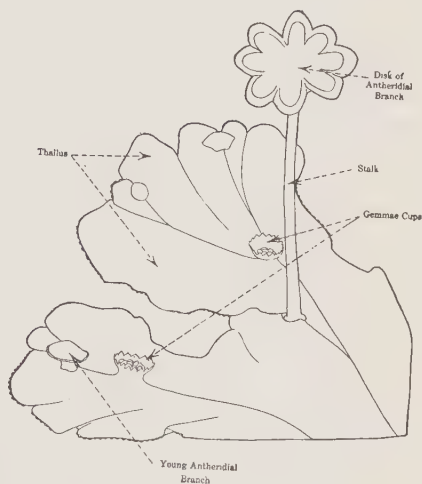


FIG. 186.—A portion of the male gametophyte of *Marchantia*, showing antheridial branches and gemmae cups. The latter are also sometimes produced on the female gametophyte.

up of a single layer of flattened sterile cells and, within this wall, a number of free spherical cells each of which divides up into a tetrad of four spores. The spores are freed by the decay or shriveling of the tissue of the gametophyte, and on germination form new gametophyte plants. The first of the two nuclear divisions by which each spore mother cell produces four spores is a reduction division by which the chromosome number is reduced to the haploid number. (See Fig. 184 for a diagram of the live cycle.)

Marchantia also has a branched thallose gametophyte, but the gametangia, which are produced on different gametophytes, instead of being buried in depressions in the thallus, are on special erect thallus branches.

The sporophyte of *Marchantia* (Figs. 185 and 186) is larger than that of *Riccia* and more complex. It consists of a **foot** which acts as an organ for attachment to the gametophyte and

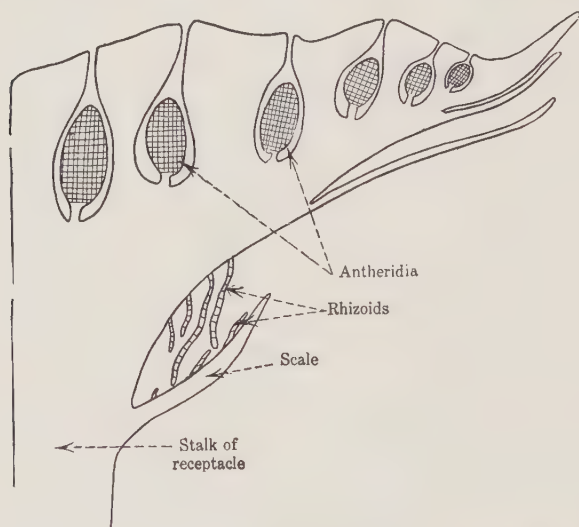


FIG. 187.—Diagram of half of an antheridial disk of *Marchantia*, showing the position of the antheridia. The antheridia are essentially the same in structure as those of *Riccia* as shown in Fig. 181 and have a wall one cell layer thick, not shown in this diagram, within which are great numbers of sperm-producing cells.

of absorption of food from it, a **stalk**, and a **capsule** within which the spores are formed. Much of the sporophyte of *Marchantia* consists of sterile cells, i.e., there is relatively much less sporogenous tissue in the sporophyte of *Marchantia* than in *Riccia*. Even within the capsule some of the cells instead of forming spores develop into peculiar sterile cells called **elaters**, which aid in spore dissemination.

In *Marchantia* there is rather effective provision for the distribution of spores, whereas such provision is lacking in *Riccia*. In the former plant the facts that the sporophyte is not buried in the gametophyte tissue, that its attachment is in a pendant position to the under side of the stalked archegonial branch, the

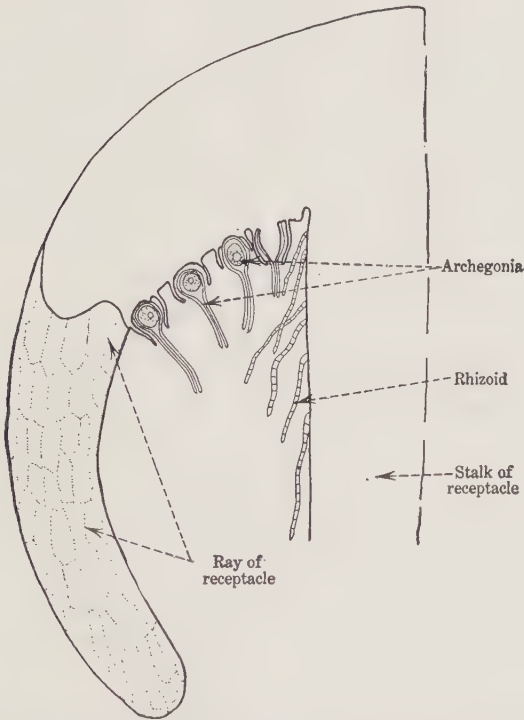


FIG. 188.—Diagram of half of an archegonial receptacle of *Marchantia*, showing the position of the archegonia.

presence of a stalk, and the presence of elaters among the spores all favor widespread dissemination of spores. In *Riccia*, on the other hand, the spores, buried within the gametophyte, escape only by the disintegration of the tissue of the latter.

In most liverworts the sporophyte is parasitic upon the

gametophyte, securing from it all its water and food. The gametophyte of many liverworts are leafy, rather than thallose, as in *Riccia* and *Marchantia*.

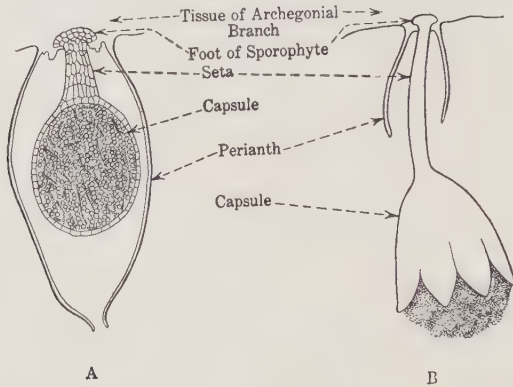


FIG. 189.—*Marchantia*. A, median longitudinal section of an immature sporophyte. B, mature sporophyte, with capsule dehiscing. In both figures, a portion of gametophytic tissue is shown. B is drawn on a smaller scale than A.

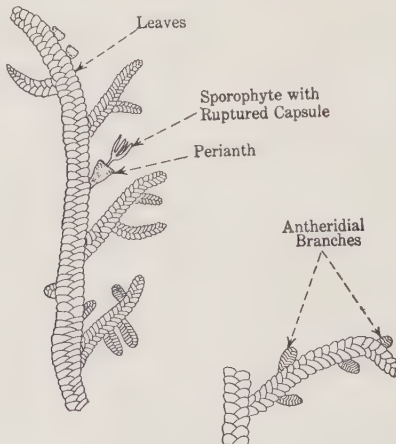


FIG. 190.—A leafy liverwort (*Porella*). At left, a portion of a female gametophyte; at right, a portion of a male gametophyte.

Although mention has been made here of but two liverworts, *Riccia* and *Marchantia*, both of which are fleshy, thallose

forms, many species of liverworts, in fact most species, are leafy like *Porella* shown in Fig. 190.

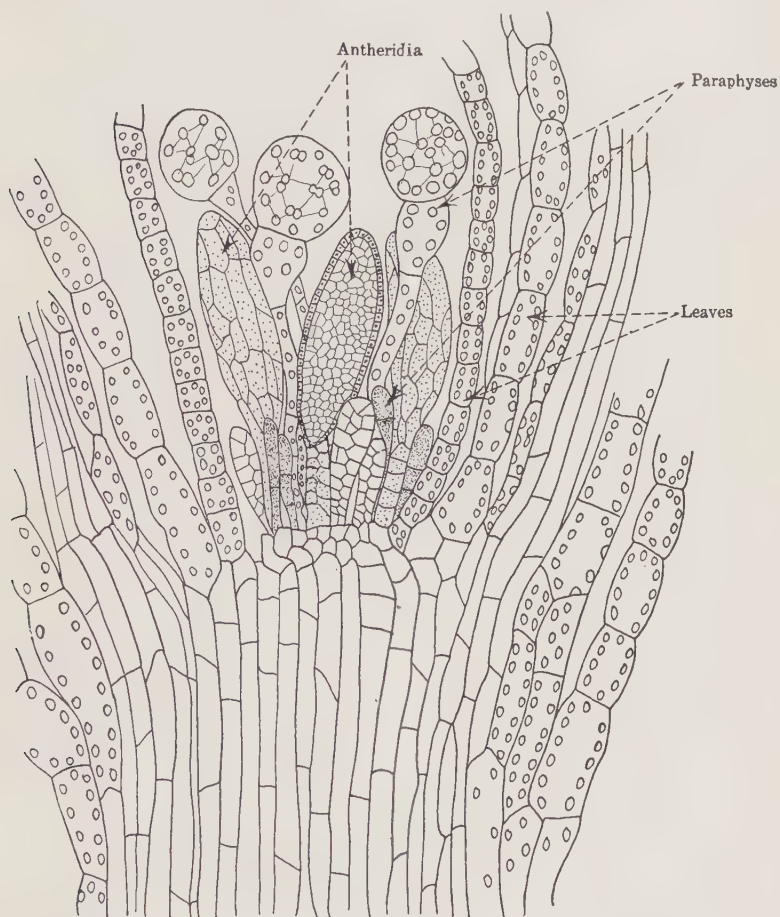


FIG. 191.—*Funaria hygrometrica*. Longitudinal section of the tip of a male branch, showing antheridia and paraphyses. (Redrawn from Sachs.)

THE MUSCI (MOSSES)

The second class of the Bryophyta includes many more genera and species than does the first class, the Hepaticae. Further-

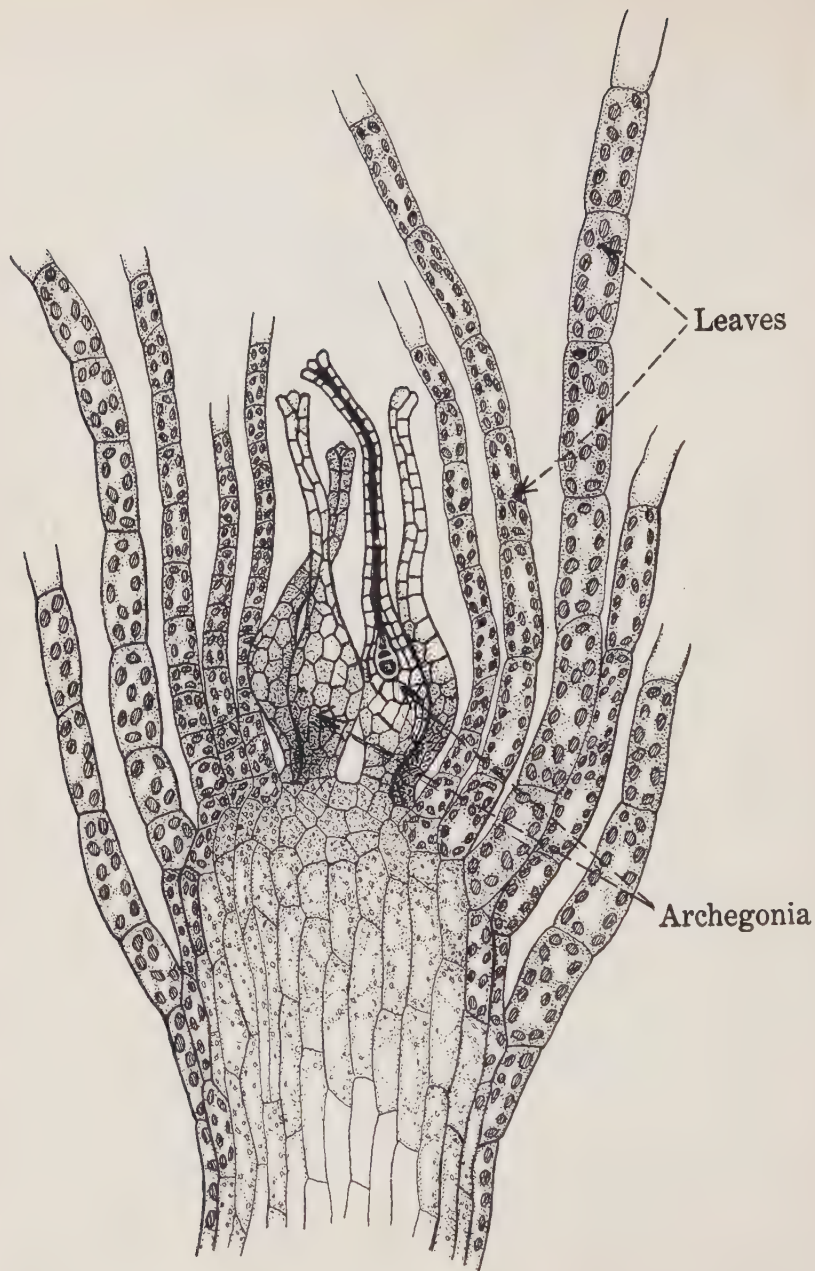


FIG. 192.—*Funaria hygrometrica*. Longitudinal section of tip of a female branch, showing archegonia. (Redrawn from Sachs.)

more, the mosses are a much more conspicuous and important element of the flora than are the liverworts. There is, however, much more uniformity in the structure of both the vegetative

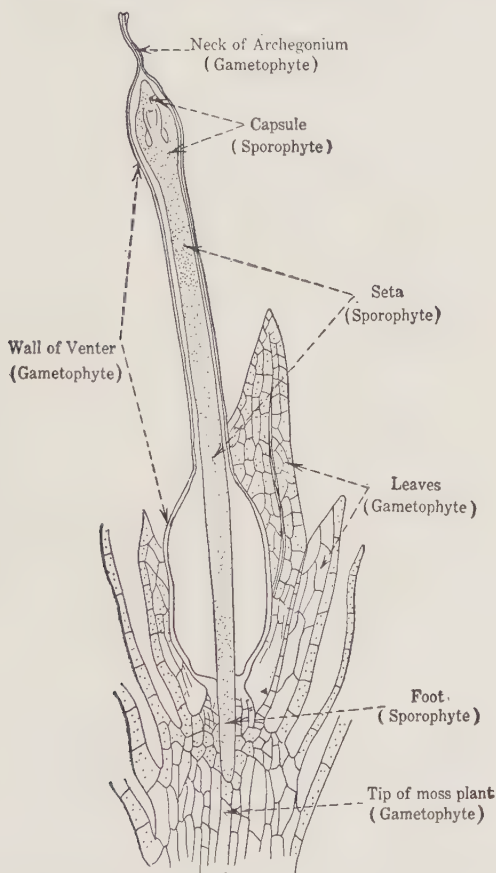


FIG. 193.—Tip of a female gametophyte branch with an advanced sporophyte as seen in longitudinal section (semi-diagrammatic). The shaded structure is the sporophyte. (Adapted from Sachs.)

and reproductive structures among the mosses than among the liverworts. The mosses are not so strictly limited to very moist habitats as are most of the liverworts. A few mosses are aquatic,

many grow upon soil, and many others upon rocks, the bark of trees, and decaying wood.

The mature gametophyte of the mosses always consists of a stem having rhizoids at the lower end and bearing spirally arranged leaves. These leaves differ from the leaves of the leafy liverworts, which are borne in two rows, not only in their spiral arrangement but also in having a midrib.

A Representative of the Mosses.—*Funaria* illustrates the principal features of the structure and development of the plants of this group.

The spores, which are produced in great numbers, are very small and well adapted to dispersal by wind. On germination, instead of giving rise directly to the leafy gametophyte, there is formed a green filament made up of cells placed end to end as in many of the green algae. This filamentous

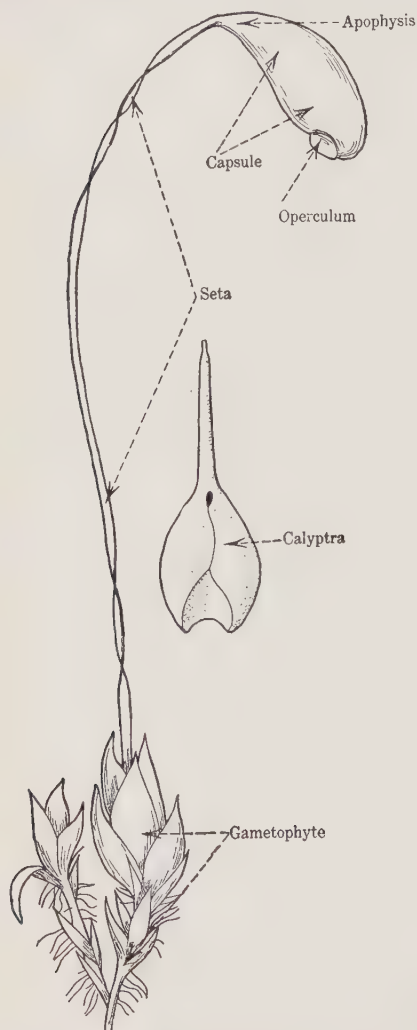


FIG. 194.—Portion of a gametophyte and attached sporophyte of a common moss, *Funaria hygrometrica*.

stage of the gametophyte which branches freely is called the

protonema (Fig. 196, 14), and, by means of numerous conspicuous chloroplasts, carries on photosynthesis which makes possible its growth. Special branches which arise from the protonema, produce erect stems bearing rhizoids at the lower end and simple leaves above. This is the stage of the gametophyte which we usually think of as "the moss plant."

At the tips of some of these erect shoots the groups of antheridia are borne, and at the tips of others are groups of archegonia. (Figs. 191 and 192.) Many sterile hairs, known as paraphyses, occur among the antheridia and archegonia. If the gametophytes are wet, the motile sperms swim to the archegonia, where fertilization occurs.

The sporophyte (Figs. 193, 194 and 195) which develops

from the zygote is a larger and more complex organ than the sporophyte of the liverwort's structure, in which the sporogenous tissue is much reduced and tissues for photosynthesis and elaborate provision for spore dissemination are present. The sporophyte consists of (a) the foot, which penetrates the tip of

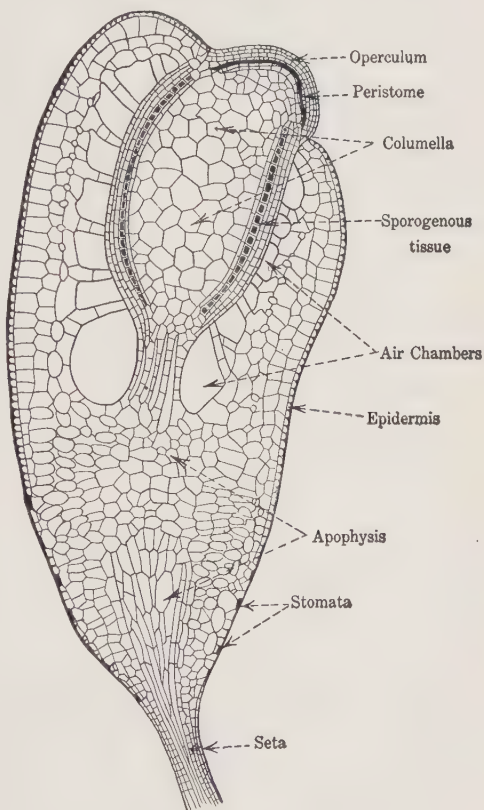


FIG. 195.—Longitudinal section of the capsule of the sporophyte of *Funaria hygrometrica*.

the stem of the gametophore and serves as an organ of attachment and absorption, (b) the stalk or seta and (c) the capsule, a complex structure within which the tetrads of spores are pro-

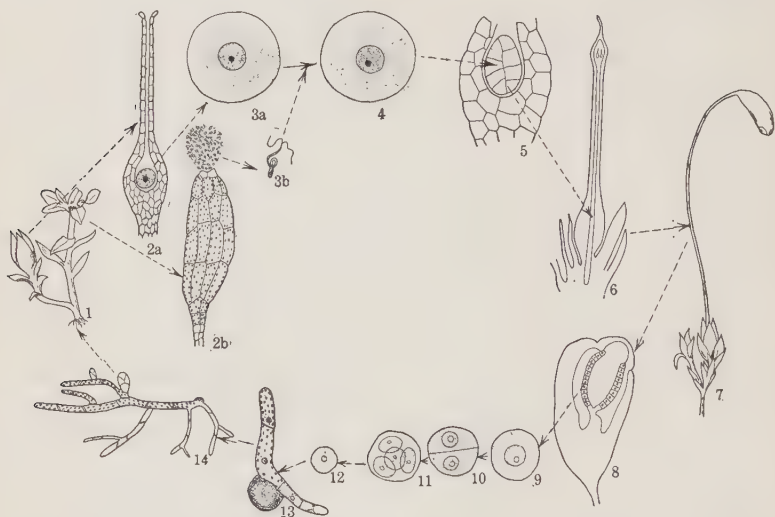


FIG. 196.—Diagram showing the life cycle of a typical moss (*Funaria*). 1, the leafy gametophyte plant (gametophore), showing an antheridial and an archegonial branch. 2a and 2b, an archegonium and an antheridium with mature egg and sperm. 3a and 3b, an egg and a sperm. 4, the zygote resulting from their fusion. 5, a young embryo sporophyte within the venter of the archegonium. 6, sporophyte in advanced stage of development, attached to the gametophyte and surrounded by the enlarged archegonium. 7, mature sporophyte attached to the gametophyte. 8, section of the sporophyte capsule showing the location of the spore mother cells. 9, spore mother cell. 10, two cells resulting from reduction division of the spore mother cell. 11, tetrad of spores resulting from division of the two cells. 12, a single spore. 13, germinating spore showing protonemal thread and rhizoid. 14, older gametophyte plant showing the buds which develop into leaf shoots of the gametophyte. The stages from 4 to 9 belong to the sporophyte generation, those from 10 to 3 to the gametophyte generation.

duced but which is mostly made up of sterile tissue. In spite of its relative complexity the sporophyte's possibilities of development are limited by reason of the fact that it is restricted in the quantity of water and salts it can secure, by the limited

ability of the gametophyte for absorption and conduction. The sporophyte must secure all its water and soil solutes through the foot, which absorbs them from the gametophyte stem in which it is imbedded.

In the next class, the Pteridophyta, the gametophyte is even simpler than in the Bryophyta, but the sporophyte is much more complex than in the mosses and liverworts. Moreover, it develops entirely new sporophyte organs, a root and a stem with leaves. The presence of a root makes it possible for the sporophyte to establish direct connection with the soil and thus secure adequate supplies of water and salts. This has made it possible for the sporophyte of ferns and higher plants to evolve into a structure of great size and complexity.

CHAPTER XIII

PTERIDOPHYTA (FERNS AND FERN ALLIES)

GENERAL CHARACTERISTICS

THE ferns and their allies constitute a large assemblage of plants which have certain resemblances to the liverworts and mosses on the one hand, and to the seed plants on the other. They resemble the Bryophyta in the following important particulars: (1) They produce ciliated male gametes; (2) they require water in order that fertilization may take place; and (3) they have gametangia which are essentially of the same structure as those of the liverworts and mosses. They resemble the Spermatophyta in that their sporophytes all have roots and can therefore live independent of the gametophyte and in that they possess well-developed vascular (conducting) tissue.

With the attainment of complete independence by the sporophyte and the accompanying increase in its complexity, there is a corresponding decrease in size and complexity of the gametophyte.

We have seen that in the Bryophyta the sporophyte is entirely dependent for its supply of water and mineral salts upon the gametophyte, which alone possesses organs (rhizoids) for absorbing water and soil solutes from the soil. In many of the Bryophyta the sporophyte is unable to manufacture any of its own food, even though supplied by the gametophyte with water and soil solutes. However, there is a certain approach to independence of the sporophyte in some mosses which have developed chlorophyll-bearing tissue and which could probably live entirely independently if they possessed rhizoids or a root.

It is nevertheless within the Pteridophyta that complete

independence of the sporophyte is first attained. Although the sporophyte of the ferns and fern allies is at first attached to the gametophyte by a foot and is for a short time dependent upon it for water and food as well, it soon develops a root which attaches it directly to the soil. By virtue of having a root, the sporophyte is no longer dependent upon the gametophyte for its supply of water and mineral salts. It also possesses leaves, organs which never occur on the sporophyte of the Bryophyta, and a corresponding development of food manufacturing tissue. This, together with a well-organized vascular system, efficient epidermis, and a root which can penetrate into the deeper and relatively moister layers of soil, has enabled it successfully to carry on an independent terrestrial existence, which is not possible for the sporophyte of any of the Bryophyta.

The roots of the Pteridophyta and Spermatophyta, although performing the same functions as rhizoids, are structurally far more complex and are capable of indefinite growth.

As to the origin of the Pteridophyta, it is the generally accepted opinion that they and the mosses represent two distinct lines of development from some liverwort ancestor. The Bryales (mosses) have the most complex and highly differentiated sporophyte of any existing plants below the Pteridophyta, but there is little ground for the assumption that the Pteridophyta have arisen from the mosses even though the mosses are in some respects intermediate between the liverworts and the ferns.

A study of fossil plant remains reveals the fact that the ferns and their allies appeared on the earth earlier than the seed plants. During the carboniferous period (geological age when the great coal beds were deposited) particularly, they were very abundant; in fact they dominated the vegetation of that time.

The Pteridophyta which exist upon the earth to-day are divided into three classes.

1. The Filicineae (Ferns).
2. The Equisetineae (Horsetails).
3. The Lycopodineae (Club Mosses).

Representatives of the Pteridophyta.—A large majority of the living pteridophytes belong to the Filicineae. These ferns are widely distributed over the surface of the earth. They flourish most luxuriantly in moist, shady habitats, but there are some



FIG. 197. —Sporophyte of Christmas fern (*Polystichum*). The horizontal rhizome is shown bearing at the tip young coiled leaves, also the expanded leaves of the previous season, each with a stalk or stipe, prolonged to form the rachis from which pinnae (leaflets) arise laterally. Fibrous roots arise from the lower side of the rhizome. The older parts of the stem are covered with the petioles of dead leaves. (After Curtis.)

species which grow in very dry situations. Ferns reach their greatest size in the tropics, where certain tree ferns grow to a height of fifteen meters or more. The stems of such tree ferns are erect, woody, and unbranched, and each bears at its apex a

cluster of compound leaves (**fronds**). Most of the ferns, however, have a horizontal or short erect stem (**rhizome**), which is developed underground (Fig. 197).

Polypodium may be selected as typical of the group. The familiar fern plant, as we know it, with its roots, stem and leaves (fronds) is the asexual or sporophyte generation. The nuclei of all the cells of this generation possess the diploid number of chromosomes. The spores are borne in sporangia, clusters of which form brownish "dots" on the under side of the frond. When the spores are formed, one of the cell divisions is a reduction division. Fronds which bear spores are spoken of as sporophylls. In *Polypodium* all fronds are spore-bearing, but in some ferns, the sporangia are definitely limited to a certain few fronds (**sporophylls**) which in some species are quite unlike the other leaves. In most of the common ferns the sporangia are borne in groups (sori) on the backs of the leaves. (See Figs. 204 and 205.) In many species, but not in *Polypodium*, there is a membranous covering (*indusium*) over each sorus. In *Polypodium* each sporangium consists of a **stalk** and a **capsule**. The wall of the capsule is composed of a single layer of cells, which are thin-walled except for the **annulus**, a row of cells extending from the stalk over the top of the capsule and part way down the other side. The inner and radial walls of the cells composing the annulus are much thickened, while the outer walls are relatively thin. Between the end of the annulus and the stalk are a few thin-walled cells, two of which, the **lip cells**, are narrow and radially elongated. At maturity the sporangium wall splits between these two lip cells. The spores are formed in tetrads (groups of four) as in the Bryophyta. The spores of *Polypodium* are all alike, and this genus is therefore said to be **homosporous**, in contrast with those pteridophytes (*Selaginella* and others) which produce two kinds of spores differing in size and other respects and which are said to be **heterosporous**.

A spore on germination forms a gametophyte, or **prothallium** (Figs. 198 and 199), which is a flat, green heart-shaped plate

of cells a few millimeters in diameter, and even simpler in structure than are the gametophytes of the bryophytes. In **monoeocious** species, as *Polypodium* species, male and female gametangia are borne on the same gametophyte; in **dioecious** species, some

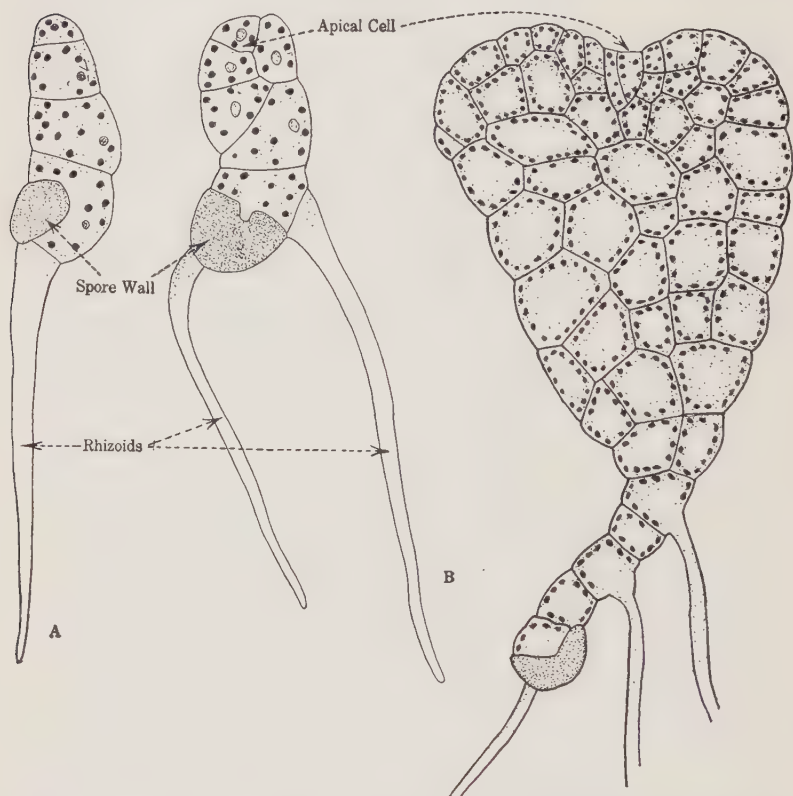


FIG. 198.—Early stages in the development of the gametophyte of *Polyodium*.
(See explanation in text.)

of the gametophytes bear only antheridia, and others only archegonia. The gametangia are borne on the under surface of the gametophyte, the archegonia near the notch of the thallus, the antheridia scattered among the rhizoids.

The sperms are released from the antheridia (Fig. 200), only in the presence of water, and fertilization of the egg cell occurs in the archegonium (Fig. 201), where the zygote remains and begins to divide at once to form an embryo.

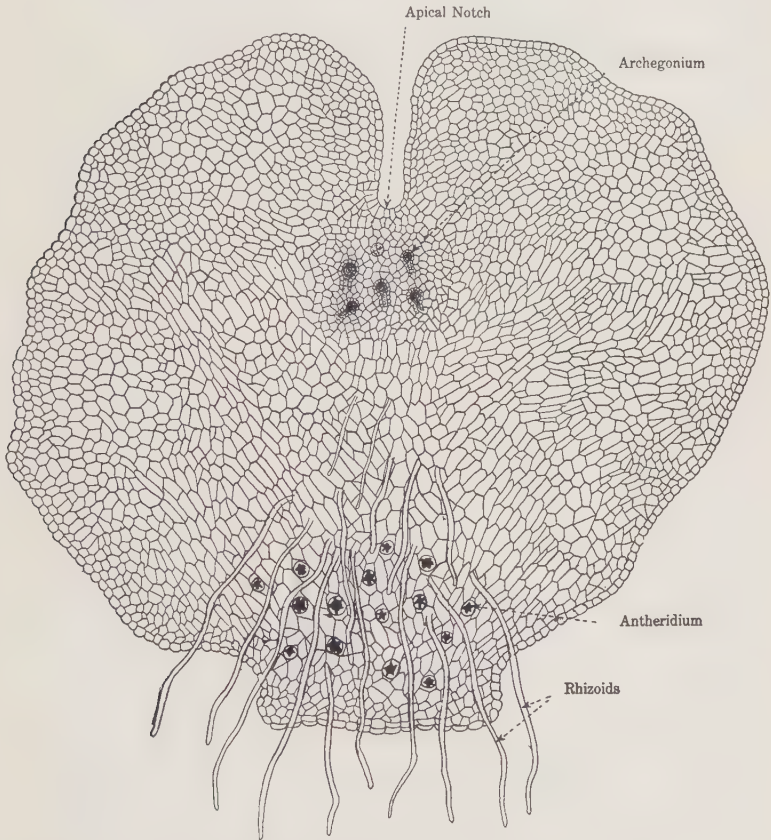


FIG. 199.—Mature gametophyte (prothallium) of a fern, as seen from the ventral surface.

The embryo or young sporophyte (Figs. 202 and 203) develops the following four primary organs:

1. The foot, which is a mass of small cells embedded in the

tissue of the prothallium (gametophyte), and which absorbs food and water for the young embryo from the gametophyte.

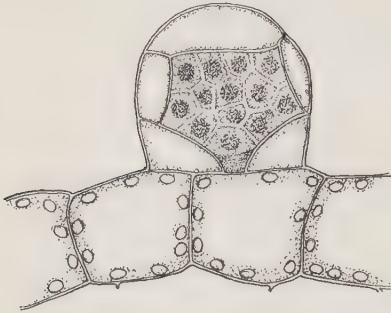


FIG. 200.—Mature antheridium of a true fern. Scale about three times that of Fig. 201. (After Atkinson.)

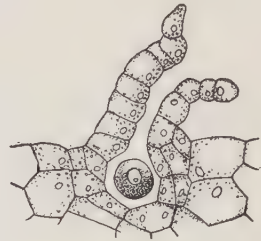


FIG. 201.—Mature archegonium of a true fern, ready for fertilization.

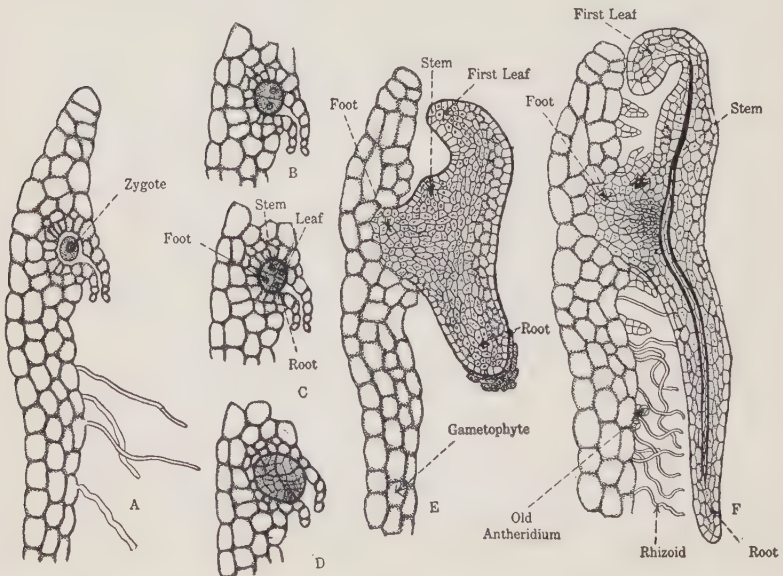


FIG. 202.—Successive stages in the development of the fern sporophyte.

2. The root, which grows downward and pushes its way into the soil.

3. The primary leaf, which, though little resembling the permanent leaves, is the first photosynthetic organ of the sporophyte.

4. The stem, which becomes the perennial rhizome from which the fronds and adventitious roots arise.

These organs develop in the order given. In the early stages of embryo development the young sporophyte is completely parasitic upon the gametophyte, just as in the case of the liverworts, obtaining its food and water through the foot. However, as soon as the primary root and leaf are developed, it becomes an independent organism. The gametophyte soon withers and then the foot ceases to function. Of the four structures mentioned above, only the stem (rhizome) is permanent. It soon develops leaves and adventitious roots, and the primary root and primary leaf die. As in the liverworts and mosses, so also in the ferns, the cells of the gametophyte, including the spores, sperms, and egg cells, have the haploid chromosome number in their nuclei whereas those of the sporophyte have twice that number. (See Fig. 206.)

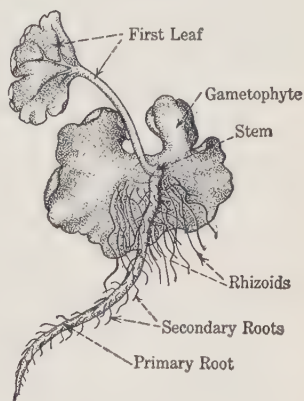


FIG. 203.—Fern sporophyte after its root has entered the soil and its first leaf has begun to carry on photosyntheses but before the death of the gametophyte.

Species of the single genus, *Equisetum* (horsetails or scouring rushes), are the only living representatives of the class *Equisetineae* (Fig. 208). There is fossil evidence that among the various species of *Equisetum* and related genera some of them were of great size and formerly constituted a much more important element in the earth's flora than do the equisetums of to-day. The living equisetums are of very distinctive form and habit. Their stems and scale leaves contain a large quantity of silica

deposited in the walls of the epidermal cells particularly, which gives these parts a characteristic harsh texture. The living species of this class are, like *Polypodium*, homosporous, not producing two kinds of spores (differing in size and in the sex of the prothallia to which they give rise) as do such heterosporous pteridophytes as *Selaginella*.

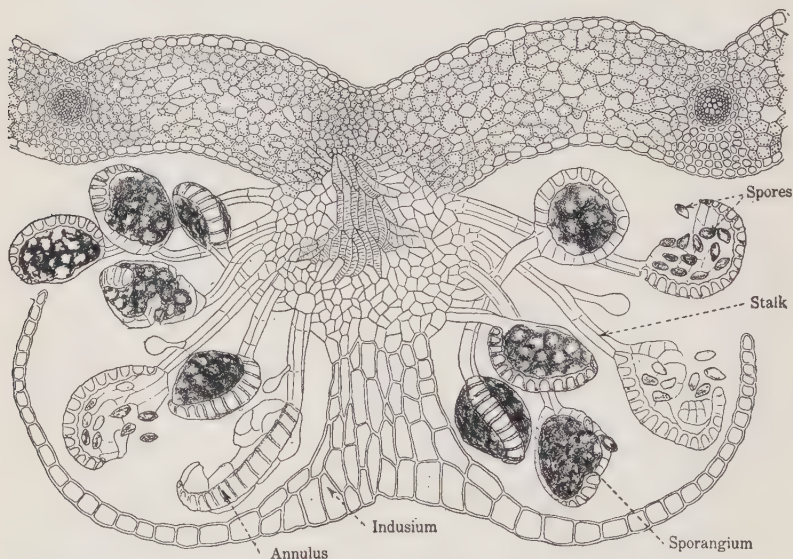


FIG. 204.—Cross section of fern leaf, through a sorus. Note the epidermal layers, chlorenchyma and veins of the leaf, as in higher plants. Different views of the sporangia are shown. (Redrawn from Kny.)

Selaginella is a type of pteridophyte showing an approach to the seed plants in having well-marked heterospory and a very greatly reduced gametophyte, even though it appears to be in some respects a much more primitive form than the true ferns. In the creeping species of *Selaginella* the shoot of the sporophyte plant is dorsiventral and the leaves are small and arranged on the axis in four longitudinal rows. Certain structures arising from the leafy stems and known as “rhizophores,” although not roots and apparently not stems since they bear no leaves,

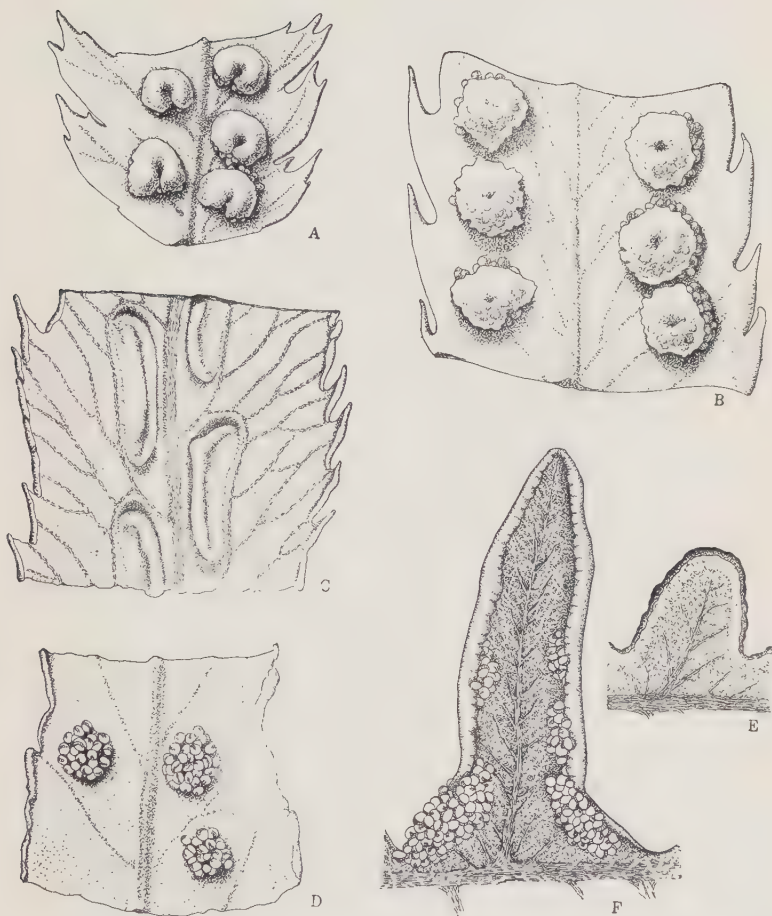


FIG. 205.—Sori and indusia of various types. *A*, sori of *Dryopteris* with kidney-shaped indusia. *B*, shield-shaped indusia of *Polystichum* sori. *C*, linear indusia covering the sunken sori of *Woodwardia*. *D*, naked sori of *Polypodium*; which are without indusia. *E*, and *F*, a young and an older pinnule of *Pteris* showing the false indusium (inrolled margin of the leaf) characteristic of *Pteris* and several related genera.

act as supporting structures and give rise to roots where they come into contact with the soil. The leaves have a loose, spongy mesophyll, and a well-developed epidermis with stomata which are usually confined to the under surface. The chloroplasts are large and few in number, and in some species there is only one in each cell. (See Fig. 209.)

The **strobili** (cone-like groups of sporophylls) are lateral branches on which the leaf-like sporophylls are borne, often in

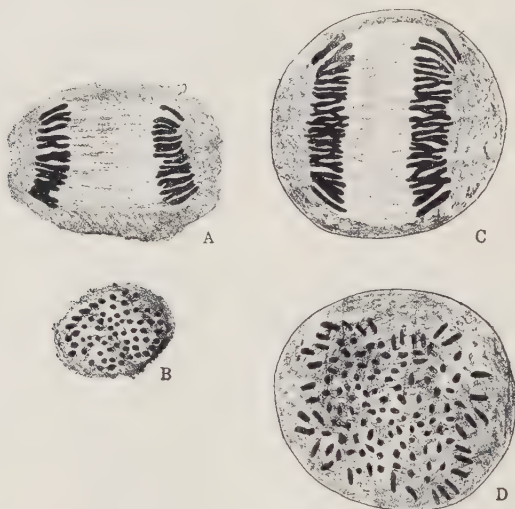


FIG. 206.—Dividing nuclei of the gametophyte (A and B) showing the haploid chromosome number, 64, and of the sporophyte (C and D) with the diploid number, 128, of the fern *Nephrodium*. (Redrawn from Yamanouchi.)

four rows so that a rather compact four-angled or club-shaped structure is formed.

Selaginella is heterosporous, although *Lycopodium* which also belongs to the Lycopodiaceae is homosporous. Both homosporous and heterosporous forms are found also among the Filicineae. Heterospory, which is the habit of producing small spores which give rise to male gametophytes and larger spores from which the female gametophytes develop, was characteristic of many of the

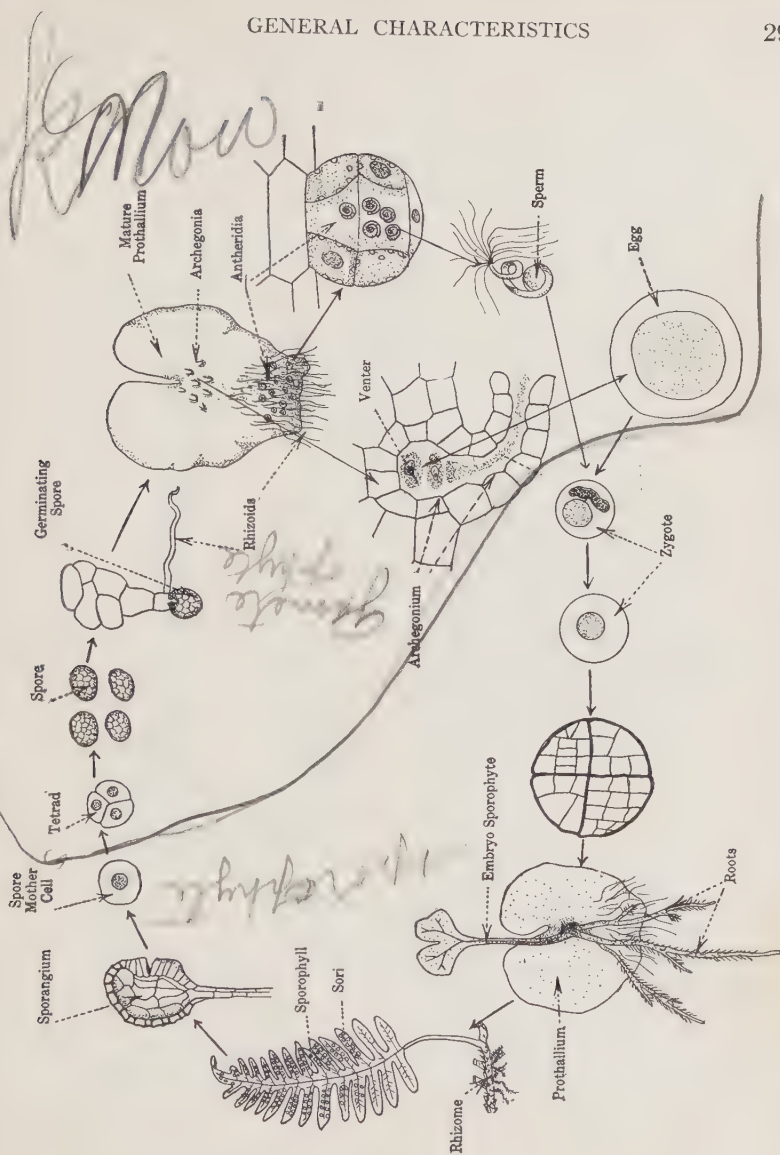


FIG. 207.—Diagrams showing stages in the life cycle of a true fern (*Polypodium*).

extinct pteridophytes. Although it is not common among living ferns and fern allies, it is universal among the spermatophytes or seed-bearing plants.



FIG. 208.—The sporophyte of common horsetail (*Equisetum arvense*), showing green vegetative shoots (*a*) and spore-bearing shoots (*b*). The aerial shoots arise from the rhizome (*r*) with tuberous storage organs; *l*, scale leaves; *sp*, sporangium. (After Curtis.)

Corresponding with the difference between the two kinds of spores (**microspores** and **megaspores**) of heterosporous plants are differences in the sporangia (**micro-** and **megasporangia**) and in

the sporophylls upon which the sporangia are borne (**micro- and megasporophylls**) (Fig. 209).

The strobili of *Selaginella* are bisporangiate in that they are made up of both microsporophylls and megasporophylls. The

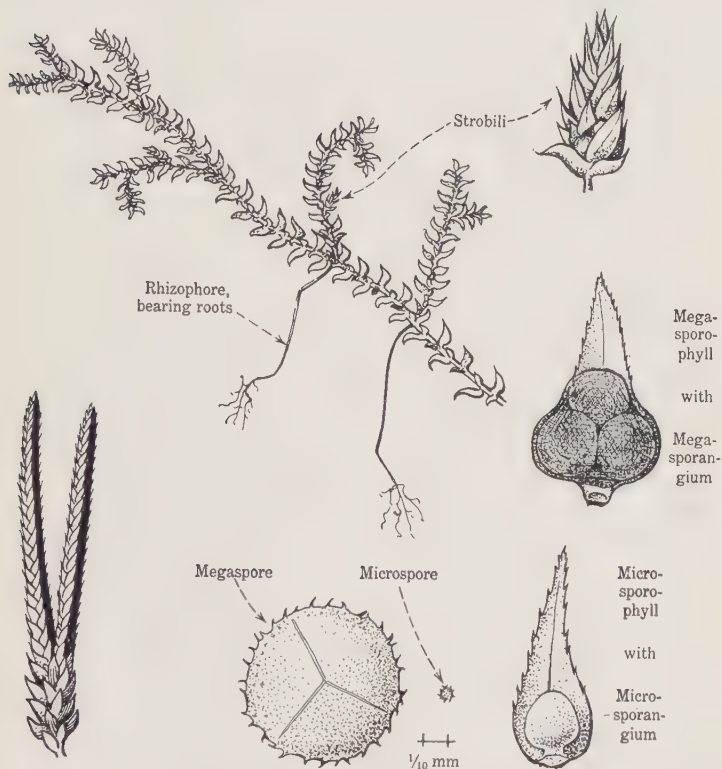


FIG. 209.—A species of *Selaginella* showing habit, strobili, microsporophyll, microsporangium, microspore, megasporophyll, megasporangium and megaspore. At the lower left hand corner are shown two strobili from a different species of *Selaginella*. The $\frac{1}{10}$ mm. scale refers only to the drawings of the spores.

groups of sporophylls (cones or strobili) of the gymnosperms are, on the other hand, monosporangiate, so that there are megasporangiate cones and microsporangiate cones. In the angiosperms, however, microsporophylls (stamens) and megasporophylls (carpels) are

phylls (carpels) are generally found together in the same group (flower).

In *Selaginella* the megasporophylls, each bearing a single megasporangium within which four large spores (the megaspores) are produced, are often located near the base of the strobilus. The microsporophylls, which are commonly found nearer the tip of the strobilus, also bear solitary sporangia (microsporangia) but each sporangium contains numerous

ous (generally sixty-four) spores (microspores).

The microspores begin to germinate before they are shed from the microsporangium. This is in marked contrast with conditions in other pteridophytes, but we shall see that in all the Spermatophyta the germination of the microspores is initiated before their release from the sporangium. The male gametophyte of *Selaginella* is formed entirely within the microspore (Fig. 210). After the division of the nucleus of the microspore, at the time of its germination, a wall is formed which divides the spores into two cells of very unequal size, the smaller of which is called the **prothallial cell**. The spores are

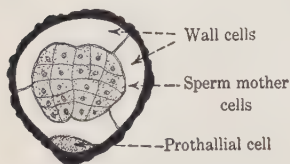


FIG. 210.—Microspore with contained male gametophyte of *Selaginella*.

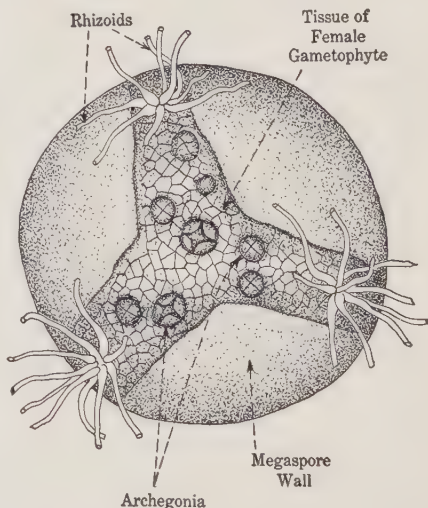


FIG. 211.—Megaspore of *Selaginella*, containing mature female gametophyte, as seen from the upper side. The wall of the megaspore has been burst by the enlarging female gametophyte which is seen protruding. (Redrawn from Bruckmann.)

usually shed while the contained gametophyte is in this two-celled condition. Subsequently the larger cell of the two goes through a series of divisions which result in the formation of a central group of cells, and a single layer of wall cells. The protoplast of each cell of the central group develops into a single sperm. The smaller cell of the first two formed

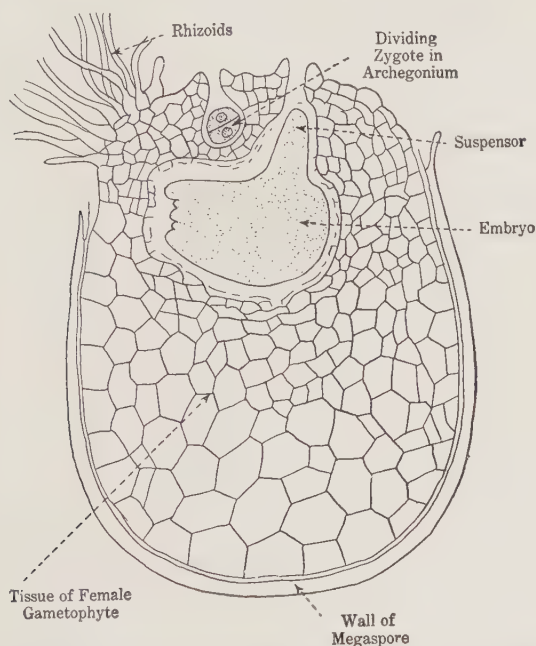


FIG. 212.—Longitudinal section of female gametophyte of *Selaginella*, protruding from the ruptured megaspore. (Redrawn from Bruckman.)

(i.e., the prothallial cell) is considered to be homologous with the vegetative cells which make up the greater part of the fern prothallium. All the rest of the gametophyte is believed to represent a single antheridium. The prothallial cell is merely a vestigial structure; it does not possess chlorophyll, and probably plays no essential part in the life history of the plant. The gametophyte is unable to carry on photosynthesis

and is entirely dependent upon the sporophyte. This is just the reverse of the condition existing in most liverworts where the sporophyte is completely dependent upon the gametophyte.

Germination of the megaspores, which generally commences before they are shed from the megasporangium, begins by the division of the single megaspore nucleus into two nuclei, between which no wall is formed. By continued **free nuclear division** (successive nuclear divisions without wall formation between the resulting nuclei), there are formed within the megaspore a

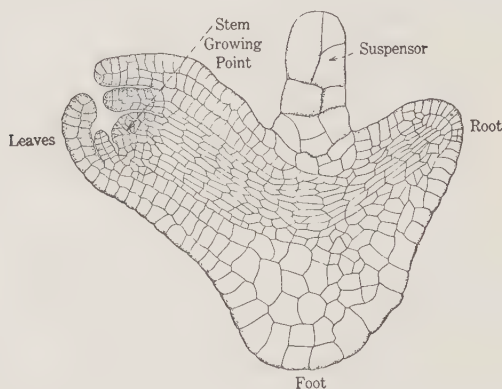


FIG. 213.—Embryo of *Selaginella*. (Redrawn after Bruckman.)

large number of nuclei most of which accumulate at one end of the spore. Then walls are formed simultaneously between the nuclei and thus a mass of tissue (the female gametophyte) is formed within the megaspore. By growth of the gametophyte the megaspore wall is finally ruptured at one end and the gametophytic tissue is exposed. Several archegonia develop in this exposed surface (Fig. 211). In some species rhizoids, which do not function, however, are produced from the exposed tissue and there may also be some development of chlorophyll in the cells of this region.

The archegonia do not differ from those of the true ferns in any important particular. All this development of the female

gametophytes takes place, at least in many species, while they are still within the megasporangium which remains attached to a megasporophyll of the strobilus, the strobilus itself being still attached to the plant.

The male gametophyte is enclosed by the microspore wall at the time when the microspores are shed and in some species of *Selaginella* the microspores when shed sift down between the megasporophylls and come to lie very near the megasporangia. If the plant is wet about this time by rain or heavy dew, the wall separating the sperms breaks down, the contents of the microspore swell, the microspore wall is ruptured, and the biciliate sperms are set free. Previous to this time the megasporangium wall has cracked open, but not sufficiently to permit the megaspore with the contained female gametophytes to escape. The sperms swim to the archegonia, which are by this time ready for fertilization. The presence of water is essential in order that the sperms may reach the archegonia, a condition which gives indication of the origin of *Selaginella* from aquatic ancestors.

The fertilized egg is the beginning of the sporophyte generation, and generally its development into an embryo sporophyte starts at once (Fig. 212). The first division of the egg is by a transverse wall and results in the formation of an outer cell known as the **suspensor cell**, and an inner cell, the **embryo cell** from which the embryo proper develops. The suspensor cell greatly elongates, pushing the developing embryo down into the deeper tissue of the female gametophyte, from which nourishment is absorbed. The suspensor cell may divide several times, but it takes no part in the formation of the embryo proper. The suspensor is a structure which distinguishes the Lycopodiaceae from other Pteridophyta, but which occurs in practically all seed-bearing plants. The young embryo, embedded in the tissues of the female gametophyte and still enclosed within the megaspore wall, consists of a foot, a rudimentary root, and a stem growing point with rudimentary leaves (Fig. 213). In some species the megaspores are not shed until after the growing

stem and root of the embryo have begun to emerge from the female gametophyte or have even forced their way out through the sporangium wall.

After the female gametophytes are shed from the strobilus the root soon enters the ground, the stem elongates, leaves are developed, and the young sporophyte becomes independent. The suspensor and foot are temporary structures.

Advance of the Pteridophyta over the Bryophyta.—The greater size and conspicuousness of ferns and their allies as compared with the mosses and liverworts seems clearly to be due to the fact that in the Pteridophyta the sporophyte generation is freed from the limitations imposed upon it in the Bryophyta by its permanent attachment to and dependence upon the gametophyte. It is obvious that so long as the sporophyte had to receive all its water and soil solutes from the gametophyte the sporophyte could not develop into a structure much exceeding the gametophyte in size or differentiation. With the emancipation of the sporophyte plant from permanent dependence upon the gametophyte by the development of a root the greater possibilities for development apparently innate in the sporophyte were, so to speak, released. With its own root system making possible firm attachment to the soil, and absorption of large quantities of water and soil solutes, the sporophyte plant was able to evolve into the large and highly differentiated structure which we know as "the plant" in the true ferns and in the flowering plants. There is some reason for looking upon the gametophyte as capable of adapting itself to the relatively simple aquatic environment but incapable of adjusting itself in the course of evolution to efficient life on land. The sporophyte, on the other hand, has been able to evolve into a structure well adjusted to the land habitat, and the gametophyte, greatly reduced in size and in complexity of structure, has in the heterosporous pteridophytes and flowering plants become completely dependent upon the sporophyte.

CHAPTER XIV

SPERMATOPHYTA (SEED-BEARING PLANTS)

THE fourth division of the Plant Kingdom, the Spermatophyta, by far exceeds in importance, both economically and as an element in the flora of the earth, all other living plants. The spermatophytes are the dominant plants of our time and exceed in number of species all the Thallophyta, Bryophyta, and Pteridophyta taken together.

The reason for the dominance of the Spermatophyta is clearly the fact that they are more effectively adapted to the land habitat than are any other plants. Although the types of the three lower divisions which we have discussed in the preceding chapters, or the groups to which they belong, certainly do not represent an actual evolutionary series which has culminated in the production of the seed-bearing plants, they probably do correspond roughly to the principal steps in the evolution of the Spermatophyta. The seed plants have in all probability descended from pteridophyte ancestors, through forms long extinct which were intermediate between certain of the living ferns and the most primitive of the Spermatophyta.

The series of progressive changes which we have traced through the three lower divisions reaches its culmination in the seed plants, for:

1. The sporophyte of the seed plants may attain a length of hundreds of feet, it has the most highly complex differentiated tissues found among plants, and it is dependent upon the gametophyte for a very short period only.
2. Although an immense number of spores may be produced,

the tissue which is devoted to spore production is generally but a very small fraction of the entire sporophyte.

3. The male gametophyte is finally reduced in the higher seed plants to three cells, and the female gametophyte to eight cells, and both derive their food entirely from the sporophyte. Antheridia and archegonia, if represented at all, are very much reduced.

4. Fertilization is not conditioned by the presence of water. The male gametophyte (shed microspore or pollen grain) is carried by wind or insects to the vicinity of the megaspore and develops a tube (pollen tube) down which the male gametes pass to the female gametophyte. Except in a few very primitive seed plants, the male gametes have no cilia. With the loss of cilia by the male gametes there disappears the last structure which gives direct evidence of the aquatic origin of the higher plants.

5. The megaspore (there is only one functional megaspore in each megasporangium) is never released from the megasporangium (ovule), but remains within it and together with the female gametophyte, the embryo sporophyte, the megasporangium wall, and sometimes a mass of nutritive tissue (the endosperm) becomes the seed.

CHIEF DISTINGUISHING CHARACTERISTICS OF SPERMATOPHYTA

The two characteristics which most sharply differentiate the Spermatophyta from all other plants are: (1) the formation of the pollen tube, and (2) the production of seeds. These two characteristics are important factors making for the success of the seed plants, first, because the pollen tube has released them from dependence upon water for fertilization and, second, because the seed is a very efficient structure for reproduction and multiplication, being so very resistant to desiccation and to great extremes of temperature that it is able to retain its vitality for many years (in some cases, no doubt, for as many as a hundred). Seeds are also well adapted for wide dissemination. Moreover, on account of the well-advanced state of development of the

embryo sporophyte within the seed and the supply of stored food available to it, the new plant after germination is able to become well established before it must become self-supporting. These facts, and the possession of very efficient organs and tissues for absorption, conduction, and conservation of water make it possible for seed plants to thrive in habitats which are much drier than those to which the Bryophyta and Pteridophyta are for the most part restricted.

The seed-bearing plants include species which are adapted to a wide range of conditions. By far the majority are autophytic, but a few are heterophytic, as for example, such saprophytes as Indian pipe (*Monotropa*) and such parasitic forms as dodder (*Cuscuta*). Autophytic seed-bearing plants are to be found in almost every location where organisms can exist at all.

The Spermatophyta consist of two well-marked classes, the Gymnospermae (gymnosperms) and the Angiospermae (angiosperms). These two class names are based upon one of the best-defined distinctions between the two groups. The seeds of the Gymnospermae (naked-seeded plants) are borne upon the surface of the megasporophyll (carpel or cone scale) (Fig. 216, *B*), while the seeds of the Angiospermae (covered-seeded plants) are always contained within a structure (the ovary) which is closed, at least until the seeds are mature, and which is formed by the union of the margins of one or more megasporophylls (carpels).

GYMNOSPERMAE

The gymnosperms are all woody, perennial forms and with few exceptions are evergreen plants. They are of great economic importance as sources of timber, rosin, and turpentine. The group is a relatively small one, including only about 500 species, whereas there are more than 125,000 species of angiosperms. Among the best known gymnosperms are the pines (*Pinus*), spruces (*Picea*), firs, (*Abies*), larches (*Larix*), junipers, frequently but incorrectly called cedars (*Juniperus*), the so-called

Douglas fir (*Pseudotsuga*), and the redwood and big tree (*Sequoia*). We shall use the genus *Pinus* as a type of this group since its life history is better known than that of any other gymnosperm.

LIFE HISTORY OF THE PINE

The Sporophyte.—The familiar pine tree is the sporophyte plant and corresponds to the attached, dependent sporophyte (foot, seta, and capsule) of a moss and to the familiar fern plant (root, rhizome, and fronds). The most striking characteristics of the pine sporophyte are as follows: (1) excurrent branching; (2) retention of the leaves during the winter; and (3) the usual grouping of the long and slender needle-like foliage leaves in clusters or **fascicles** of from two to five. Excurrent branching and the evergreen habit are characteristics shared with most gymnosperms, but the fascicles of leaves closely held together at the base by a circle of scales is peculiar to the pines. As in most of the common gymnosperms, the wood contains no tracheal tubes, but consists chiefly of tracheids with many bordered pits. The linear form of the leaves, their very thick cuticle, and the depressed stomata show the pines to be xerophytic plants, as in fact are the majority of gymnosperms.

The Strobili.—The sporophylls are borne in strobili or cones, as in *Selaginella*, but megasporophylls and microsporophylls are not found in the same strobilus, as they were in *Selaginella*. Instead there are two kinds of strobili, megasporangiate (Figs. 214 and 215), and microsporangiate (Figs. 217 and 218). Because of the names commonly used for the megasporophylls (carpels) and for the microsporophylls (stamens) among the true flowering plants (angiosperms), the two kinds of strobili in the gymnosperms are often spoken of respectively as **carpellate** and **staminate** strobili or cones. They are borne upon the same individual plant.

Megasporangiate Strobili and Megasporophylls.—The familiar pine cones are the carpellate or megasporangiate strobili.

They remain on the tree for the greater part of two years in all pines, and in some for many years. These cones first make their appearance at the beginning of the growing season when the parts within the buds develop and growth in length of the twigs begins.



FIG. 214. Tip of a branch of Monterey Pine (*Pinus radiata*), showing two megasporangiate strobili (carpellate cones) a short time after their appearance in the spring and about the time pollination takes place.

At that time there may be found near the tips of certain branches the newly formed miniature cones (Fig. 214). They seldom exceed a centimeter in length and are generally deep red or flesh color. They consist of a central axis upon which the megasporophylls are spirally arranged. If one of the megasporophylls is removed

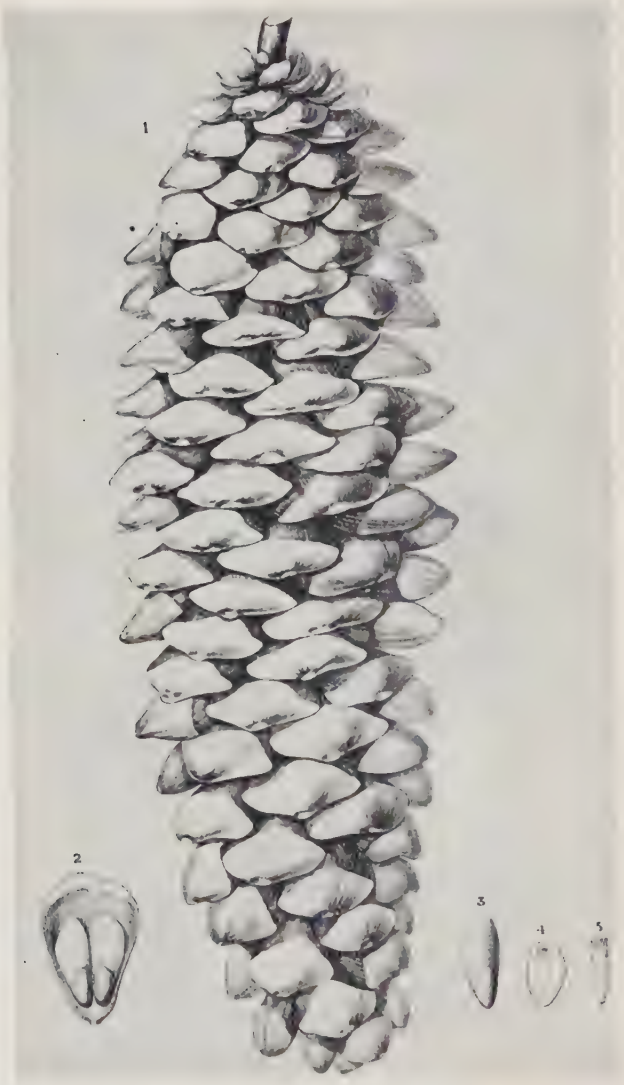


FIG. 215. Sugar pine (*Pinus lambertiana*). 1, mature cone; 2, single carpellate scale with two seeds attached; 3, single mature seed; 4, longitudinal section of seed, showing embryo embedded in endosperm; 5, embryo separated from seed, showing many cotyledons. (After Sargent from *Silva of North America*.)

from a strobilus and examined with a lens, it will be found to consist of a very short stalk and a scale to which a **bract** is attached on the lower side (Figs. 216*A* and 219*A*). On the upper side and near the base of the scale are two rounded or oval swellings. These are the megasporangia, or **ovules**, which eventually become the seeds. Sections cut lengthwise through

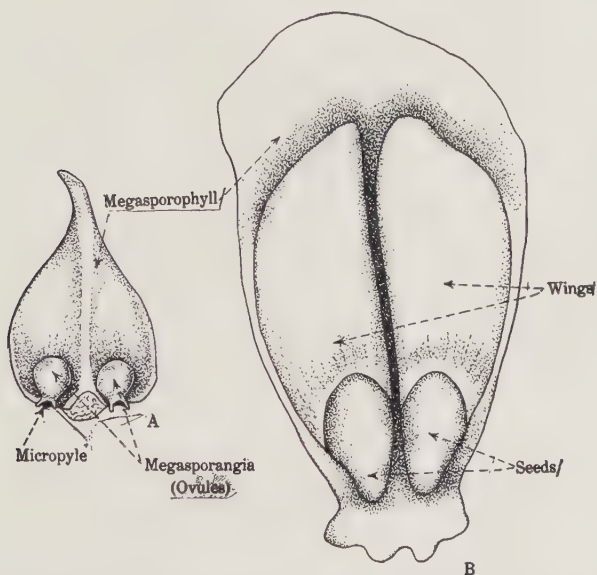


FIG. 216.—Megasporophylls of *Pinus*. *A*, about the time of pollination. *B*, after the seeds have matured. Note that the two drawings are made from different species.

an ovule show that it consists of an oval mass of tissue (the nucellus) surrounded by a single **integument**; the micropyle is directed toward the base of the scale (Fig. *A*). At the opposite end from the micropyle the tissue of the integument and nucellus is continuous with that of the scale.

Microsporangiate Strobili and Microsporophylls.—The staminate or microsporangiate strobili are produced in much larger numbers than the carpellate cones and are smaller in size. They

are found in clusters near the ends of some of the branches. Like the megasporangiate strobilus, the microsporangiate strobilus



FIG. 217. Tip of a branch of *Pinus* bearing microsporangiate strobili (staminate cones). The strobili near the base of the cluster have already shed part of their pollen while in those in the upper part of the cluster the microsporophylls have not separated and no pollen has been liberated.

consists of a short axis upon which are arranged the microsporophylls in a spiral fashion. They make their appearance at the

beginning of the growing season. The microsporophyll consists of a stalk which bears at the end an expanded scale-like portion. The two microsporangia (**pollen sacs**) are attached to the under side of this scale and to the side of the stalk. Generally the

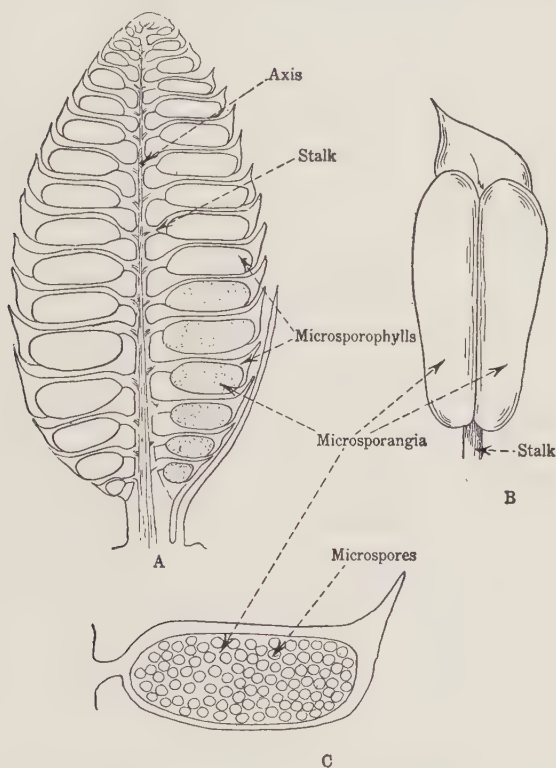


FIG. 218.—Microsporangiate strobilus and microsporophylls of *Pinus*. *A*, strobilus in longitudinal section. *B* and *C* two views of a microsporophyll, the later in longitudinal section.

microspores (**pollen**) are shed within a few weeks after the strobili have made their appearance, whereupon the strobili, having performed their function, wither and soon fall from the tree.

Megasporangium and Megaspores.—Quite early in the development of the cone, sections of the nucellus of the megasporangium show near its center a single cell which is considerably larger than the surrounding cells and has dense cytoplasm and a large nucleus. (See Fig. 219 *A* and *B*.) This conspicuous cell within the nucellus of *Pinus* soon undergoes two successive

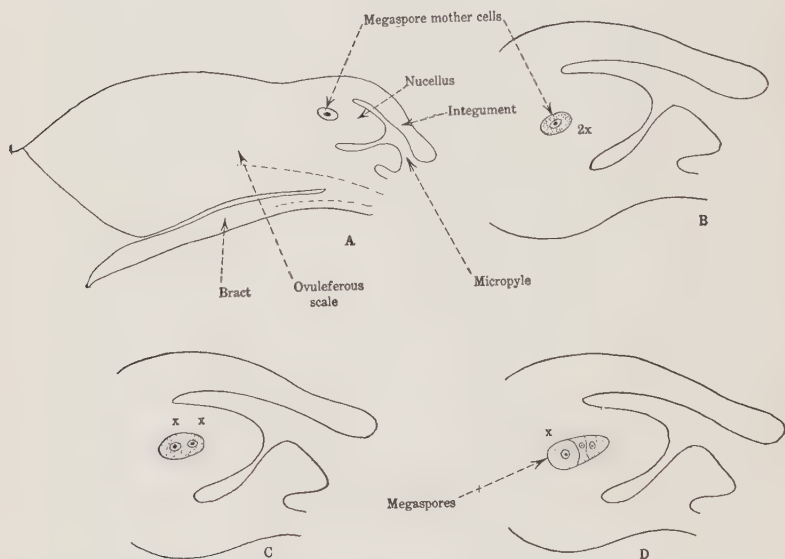


FIG. 219.—Diagrams showing the megasporophyll of pine in longitudinal section and the production of megaspores from the spore mother cell. (*A*, redrawn after Coulter and Chamberlain.)

divisions, producing four megaspores. The first division marks the beginning of the gametophyte generation, since it is a reduction division reducing the chromosome number from 24 (the diploid number) to x (the haploid number). Instead of being arranged in a tetrahedral group as are the spores of all the Bryophyta and Pteridophyta and the microspores of the seed plants, these four spores lie in a row as shown in Figs. 219*D* and 220). One of the four megaspores, the one farthest

from the micropyle, now enlarges at the expense of the other three, which are finally completely absorbed; thus only one functional megaspore is produced in each megasporangium.

Microsporangium and Microspores.—The development of the microspores within the microsporangia (Fig. 218), in *Pinus* is not essentially different from the corresponding process in *Selaginella* or from spore production in the true ferns.

The sporangium wall consists of several layers of cells, surrounding a group of sporogenous cells having, as do all the cells of the pine tree as we ordinarily know it, diploid nuclei. By the two successive divisions of each of the cells of this group there result the many tetrads of microspores, the nuclei of which have the haploid chromosome number (Fig. 221 *A* and *B*).

Germination of Microspores and Development of Male Gametophyte.—

The pollen grains or microspores of *Pinus* germinate (that is, undergo nuclear divisions) as much as a month before they are shed from the microsporangia and months before the germination of the megaspore.

The microspore just before its germination consists of an oval cell with a single large nucleus (Fig. 221 *C*). Each microspore has two balloonlike wings which are formed by the separation of the outer layer of the wall from the inner at two places and an inflation of the spaces thus formed between the two layers. The wings are air-filled and each may be almost as large as the spore proper. Of the two nuclei formed by the first division of the single nucleus of the spore, one becomes flattened out

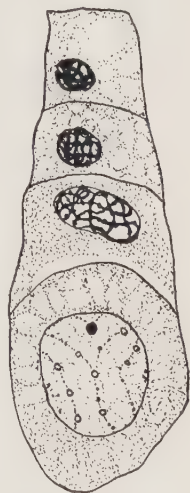


FIG. 220.—*Pinus austriaca*. Four megaspores which have arisen by the divisions of the megaspore mother cell within the nucellus. The large basal cell is farthest from the micropyle and is one which gives rise to the female gametophyte. (Redrawn after Ferguson.)

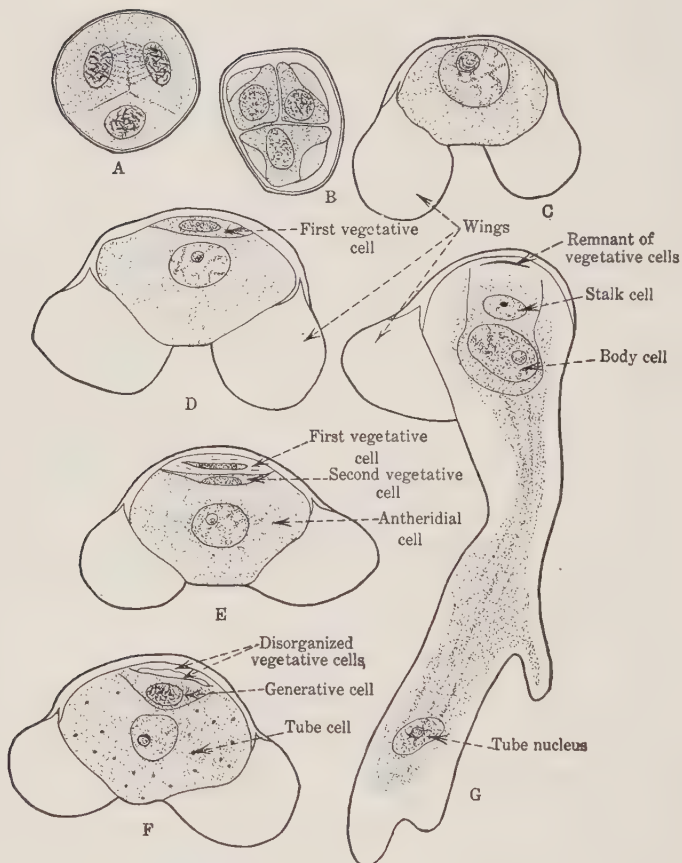


FIG. 221.—Successive stages in the development of the microspore and male gametophyte of *Pinus laricio*. A, showing the telophase of the second division of the spore mother cell. B, showing three of the four spores of a tetrad some time before maturity. C, a mature microspore. D to F, successive stages in the development of the male gametophyte up to the time the spores are shed. G, about a year after pollination and some time before fertilization. (Redrawn from Coulter and Chamberlain.)

against the spore wall and is soon cut off from the other daughter nucleus and from most of the cytoplasm of the spore by a thin cell wall (Fig. 221 *D*). This nucleus, which we shall call the **first vegetative nucleus**, rapidly degenerates. Its sister nucleus has meanwhile undergone a second mitosis. Of the two resulting nuclei, one is the **second vegetative nucleus** and behaves like the first vegetative nucleus, and the other, together with the cytoplasm surrounding it, is called the **antheridial cell** (Fig. 221 *E* and *F*). The two vegetative cells apparently perform no function but are merely vestigial cells corresponding to the vegetative cells which make up the greater part of the gametophyte of the ferns and to the single vegetative cell of the male gametophyte which develops within the microspore of *Selaginella*. A little before the microspores are shed the antheridial cell undergoes division into a smaller cell (the **generative cell**), cut off against the second vegetative cell, and a larger cell (the **tube cell**) (Fig. 221 *F*).

Pollination.—About this time the microsporangia dehisce longitudinally and the pollen grains (microspores) are liberated. The pollen is produced in astonishingly large quantities (that shed by a single Scotch pine may be as much as a liter) and the pollen grains may remain floating in the air for a long time. There are records of pine pollen having been borne for hundreds of miles by the wind.

As in all wind-pollinated plants, by far the greater part of the pollen is wasted. Some does, however, reach the carpellate cones, the megasporophylls of which at this time are slightly separated, so that some of the microspores sift down between them and come to lie in close proximity to the micropyles of the ovules. Just at this time the nucellus in each ovule exudes a quantity of a sticky fluid, which protrudes through the micropyle and comes in contact with some of the microspores. As the drop dries, the pollen grain or grains are drawn down through the micropyle and come in contact with the nucellus itself. Pollination is different from that of the angiosperms in that the pollen

grain, instead of being brought into contact merely with the stigma (tip of the carpel or carpels), is in *Pinus* and many related gymnosperms brought into direct contact with the nucellus of the ovule.

Subsequent Changes up to Fertilization.—At the time of pollination the pollen grain contains a male gametophyte consisting of two flattened and much disorganized vegetative cells, the generative cell and the tube cell (Fig. 221 *F*). The ovule at this time is in the condition already described, the nucellus or megasporangium proper being surrounded by a single integument and enclosing a single functional megaspore which is larger than the surrounding cells but lacks any thick spore wall such as is found in *Selaginella*.

Very soon after pollination the scales of the carpellate cone become closely pressed against each other as a result of their growth and they become sealed together by an exudation of pitch. Later the cone is inverted by the curvature of its stalk. During the subsequent eleven months the male gametophyte does not develop to any considerable extent. A short pollen tube is formed by each pollen grain. This tube, which may branch somewhat, penetrates the tissue of the nucellus and grows downward very slowly until cold weather comes on.

Development of Female and Male Gametophytes.—During the year following pollination there is developed from the megaspore a considerable mass of tissue which is the female gametophyte, and is often spoken of as the endosperm.

In the development of this female gametophyte, or endosperm, the megaspore first enlarges considerably at the expense of the nucellar tissue which surrounds it. It then germinates, i.e., undergoes division of its nucleus into two nuclei. These two nuclei are not separated by a wall, however, and they undergo repeated division without wall formation. After this **free nuclear** division has continued for some time, walls are formed between the nuclei and there results a solid mass of gametophyte tissue which has displaced a considerable amount of the tissue of the nucellus.

Late in the spring of the following year (nearly a year after pollination) there are formed at the end of the female gametophyte nearest the micropyle a number of archegonia, generally two or three (in some species of gymnosperms as many as sixty), which are quite different in appearance from those of the Pteridophyta. Each archegonium has its origin in a single superficial

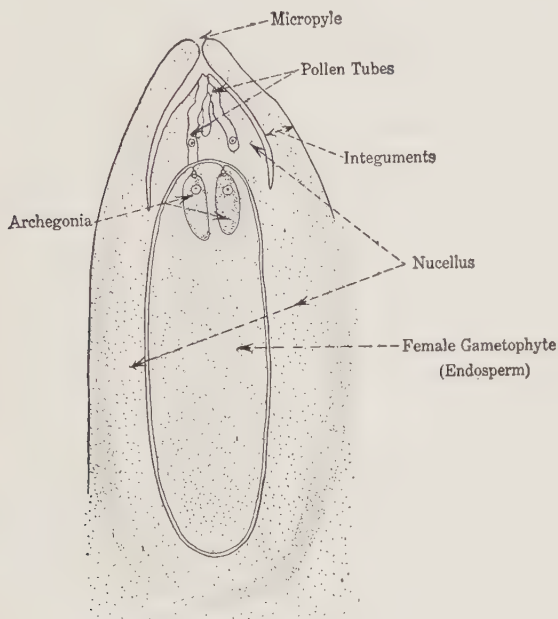


FIG. 222.—Ovule of pine at about the time of fertilization. (Redrawn after Coulter and Chamberlain.)

cell of the gametophyte, and no part of it projects above the surface of the gametophyte (Fig. 222). The cavity in which the egg lies is surrounded by a layer of cells, the **jacket cells**, which have dense cytoplasm and large nuclei. The jacket cells supply food to the egg cell and later to the embryo. The archegonium is not fully developed and ready for fertilization until about a year after pollination.

During the second spring the pollen tube, which had ceased development during the cold winter months, begins growing slowly downward and penetrating the nucellar tissue which caps the apical portion of the female gametophyte. The tube nucleus has by this time passed from the body of the spore into the tube. Meanwhile the generative cell has divided into a **stalk cell** and a **body cell** (Fig. 221 *G*), which also soon pass into the tube. In the tube the nucleus of the body cell divides into two nuclei which are the **sperm nuclei** and correspond to the sperms of *Selaginella* and other Pteridophyta and of the Bryophyta. Thus the fully developed male gametophyte consists of two disorganized vegetative cells in the body of the spore and four cells which lie in the tube and are not separated from each other by cell walls. The cells in the tube are (1) the tube cell, (2) the stalk cell, and (3) two male or sperm cells. The nuclei of the gametes (sperm cells) are large and stain more densely than do the other nuclei in the tube, and their cytoplasm is quite clearly differentiated.

Fertilization.—When the tip of the pollen tube reaches the surface of the female gametophyte, it discharges the four cells which it contains into the cytoplasm of the egg.

The nucleus of one (the functioning) male cell now moves toward the large egg nucleus which lies deep in the cytoplasm of the egg cell, and fusion of the two gamete nuclei takes place. The non-functioning male nucleus and the tube and stalk nuclei soon undergo disorganization, their material becoming part of the food store of the zygote.

Formation of the Embryo.—Immediately upon the fusion of the functioning male nucleus and the egg nucleus, the zygote nucleus begins to divide. By these divisions sixteen cells (four tiers of four) are produced, of which the uppermost four are not cut off from the cytoplasm of the egg (Fig. 223, 4, 5, 6). This group of sixteen cells is called the **pro-embryo**. Of the four tiers of cells of the pro-embryo, those in the next to the lowest tier elongate to ten or twelve times their original length (Figs. 224 and 225 *A*). They are called **suspensor cells** and their elongation

causes the four cells of the lowermost tier to be pushed deep down into the endosperm (female gametophyte tissue) below the archegonium. The eight cells of the two upper tiers remain within the cavity of the original egg cell and serve to absorb food for the nourishment of the four embryo cells, each of which

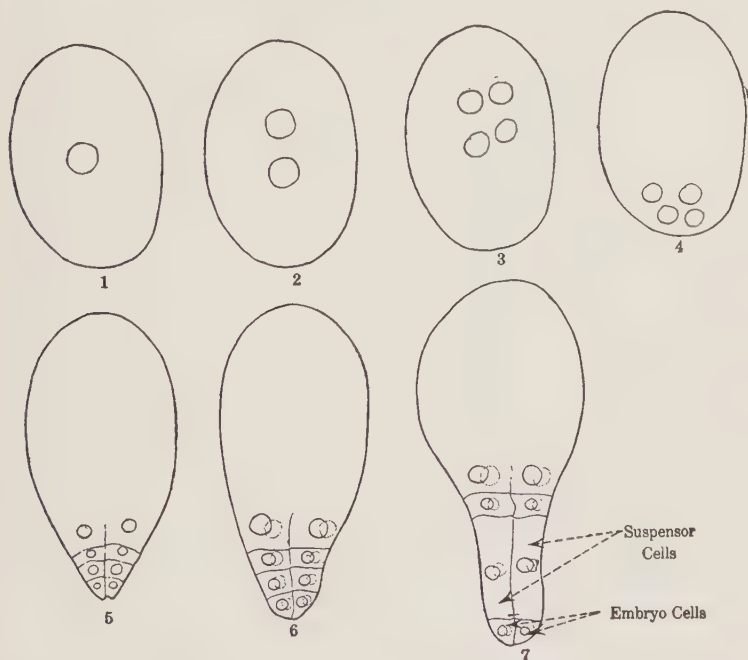


FIG. 223.—Diagrams showing stages in the development of the proembryo of *Pinus* from the zygote; 1, shows the zygote before the first division of the fusion nucleus; 2 to 7, see explanation in the text.

develops into an embryo. Since there may be three archegonia within a single pine ovule, as many as twelve young embryos may thus be formed. Before their development has progressed far, one generally surpasses the others and finally develops at their expense into the one functioning embryo of the seed.

The Seed.—Even after fertilization the endosperm continues to grow, encroaching upon the tissue of the nucellus and absorbing

it. Accordingly, in the ripe seed nothing remains of the nucellus but a brown, papery layer capping the endosperm at the micropylar end of the seed. Buried in the endosperm of the mature seed is the embryo, which consists of the **radicle**, the **hypocotyl**,

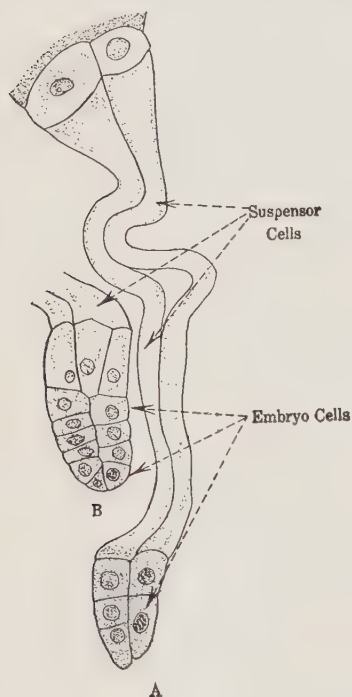


FIG. 224.—Further development of the proembryo of pine, showing early stages (A and B) in the development of the embryos. (Redrawn after Coulter and Chamberlain.)

three to eight **cotyledons**, and the **plumule** (Fig. 225 B). The shell, or seed coat, of the pine seed is formed by changes in the tissue of the integuments. In many pines a layer of tissue from the upper surface of the cone scale splits off to form a wing, which remains attached to the base of the seed when it is shed. This imparts a spinning motion to the seed as it falls, and slows up its rate of descent so that in a moderate breeze the seeds may be carried some distance from the tree on which they are produced. The germination of pine seeds does not differ in any very significant particular from that of the angiosperm seeds discussed in an earlier chapter.

After fertilization and while the ovule is developing into a seed, the whole carpellate cone grows to many times its previous size and the tissues of the cone scales

become woody and hard and lose most of their water. In most species the scales separate after the seeds have become mature, and allow the seeds to escape.

Comparison of *Selaginella* and *Pinus*.—1. The sporophyte of *Pinus* is very much larger, longer lived, more complex,

and better adapted to terrestrial life than that of *Selaginella*.

2. Megasporangia and microsporangia are produced on different strobili in *Pinus* and on the same strobilus in *Selaginella*.

3. The male gametophyte of *Pinus*, though it has two vegetative cells as compared with one in *Selaginella*, is simpler than

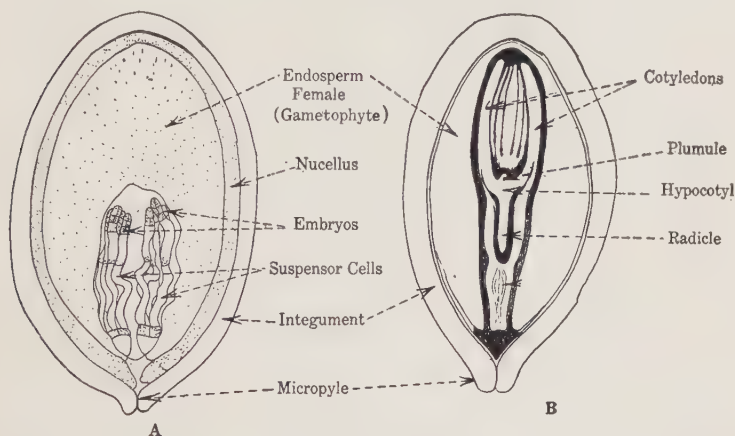


FIG. 225.—Two stages in the development of the pine seed shown in longitudinal section. *A* is much more highly magnified than *B* and shows a much earlier stage of development. Note the numerous embryos in *A* and the single surviving embryo in *B*, also the great relative reduction of the nucellus in the older seed. (Redrawn from Curtis.)

that of *Selaginella*, for it lacks any definitely organized antheridium.

4. In *Pinus* the male gametes are not ciliated and pass down a pollen tube to the archegonia; in *Selaginella* they are ciliated and swim in water to the archegonia.

5. There is but a single functioning megaspore in each megasporangium of *Pinus*, while in most species of *Selaginella* there are four.

6. The megaspores of *Selaginella* finally leave the megasporangium—even though this may not take place until after

germination, fertilization and embryo formation have taken place. In *Pinus* the megaspore never leaves the megasporangium.

7. The archegonia of *Pinus* are even simpler and more reduced than are those of *Selaginella*.

8. In *Selaginella* only a short period intervenes between liberation of the microspores and fertilization, while in *Pinus* almost a year passes between pollination and fertilization.

9. In *Pinus* the zygote gives rise to four embryo sporophytes; in *Selaginella* to only one.

10. *Selaginella* gives rise to no such structure as the seed of *Pinus* which consists of embryo sporophyte, female gametophyte (endosperm), and part of the tissue of the megasporangium.

ANGIOSPERMAE

The second class of the Spermatophyta, the Angiospermae, far exceed in number of species and in their importance to man any other class in the Plant Kingdom. In fact, in the number of known species the angiosperms exceed all the other plant groups taken together. With the exception of certain gymnosperms which furnish timber, turpentine, and rosin, the group contains the vast majority of plants that are utilized by man as a source of food, clothing, or materials for use in industry and in arts. Although angiosperms include some very simple forms, which have evolved by reduction from more highly differentiated forms, without question they represent the highest point in the evolution of plants.

The angiosperms as a class are better adapted to the land habitat than any other class of plants. Accordingly they are not only the most important and conspicuous element in the flora of the earth but are represented in practically every part of the world where plants can live at all.

Distinctions between Gymnosperms and Angiosperms.—Although angiosperms have much in common with the gymnosperms, the two classes are quite distinctly marked off from each other. The principal points of contrast are:

1. Whereas the gymnosperms are all woody, perennial plants, the angiosperms also include, in addition to such forms, many herbaceous annual and biennial plants.

2. In typical angiosperms microsporophylls (stamens) and megasporophylls (carpels) are borne together in groups (flowers), while in the gymnosperms, as we have already learned, they are borne in different groups (staminate and carpellate strobili).

3. With very few exceptions, tracheal tubes occur in the xylem of all angiosperms, but they are lacking in the xylem of all living gymnosperms except the Gnetales.

4. Angiosperm seeds are borne within a closed structure (ovary), presumably resulting from the fusion of the edges of one or more megasporophylls while the seeds of the gymnosperms almost always are borne naked on the surface of megasporophylls, which do not form ovaries.

Life History of Wheat (*Triticum*).—Among the several thousand genera of angiosperms there is for the most part marked uniformity in the essential stages in their life history. As the angiosperm representative, we have chosen *Triticum aestivum* (common wheat), not only because its life history has been rather completely worked out, but also because it is one of the most important and familiar plants in the world.

As in the Pteridophyta and in Gymnospermae, the sporophyte of wheat, and of the other angiosperms, is the conspicuous generation in the life history, i.e., the sporophyte is "the wheat plant." It consists of root and shoot, the latter made up of the stems and leaves. In addition to foliage leaves there are floral leaves.

The principal features of the grass flower referred to on page 142 (Fig. 100). The accessory flower parts, sepals and petals, are absent or greatly reduced. The stamens and carpels of all angiosperms correspond to the microsporophylls and megasporophylls of *Pinus* and *Selaginella*. In this chapter we shall use the terms microsporophylls and megasporophylls, rather than the terms stamens and carpels which originated long before

the homology of these structures with the spore-bearing leaves of the gymnosperms and pteridophytes was first suspected.

Microsporophylls and Microsporangia.—The anther consists at first of a small mass of meristematic cells (Fig. 226). There are early differentiated in this mass four separate groups of cells,

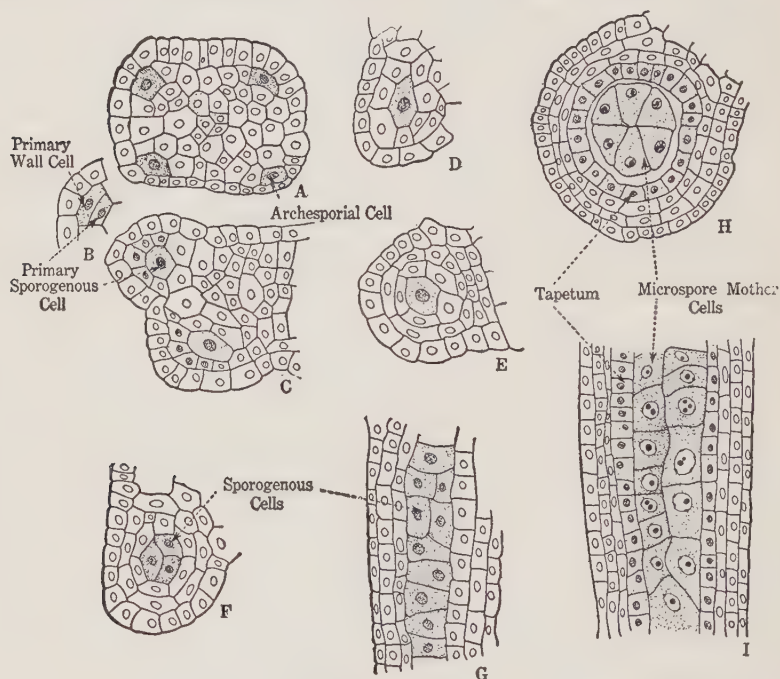


FIG. 226.—Stages in the development of the anther of wheat. *A*, cross section of a young anther. *B*, first division of an archesporial cell. *C*, *D*, *E* and *F*, cross sections of anthers showing subsequent development. *G*, longitudinal section of *F*. *H* and *I*, cross and longitudinal sections of a locule of a young anther, showing mature microspore mother cells. (Redrawn from Percival.)

which by further development will become the microsporangia. Each of these groups of cells includes a longitudinal row of cells (the **archesporial cells**) which are just beneath the epidermis and which are conspicuous by reason of the dense appearance of the cytoplasm and their large nuclei. Each cell of this row

divides, by a wall parallel to the surface of the anther, to form two cells. Thus two rows are produced. By further division of the cells of the outer row, several layers of cells are formed, and these, together with the epidermis, make up the wall of the microsporangium. By repeated division of the cells of the inner of the two original rows, cells are formed each of which gives rise to four microspores (pollen grains). The microspores are produced

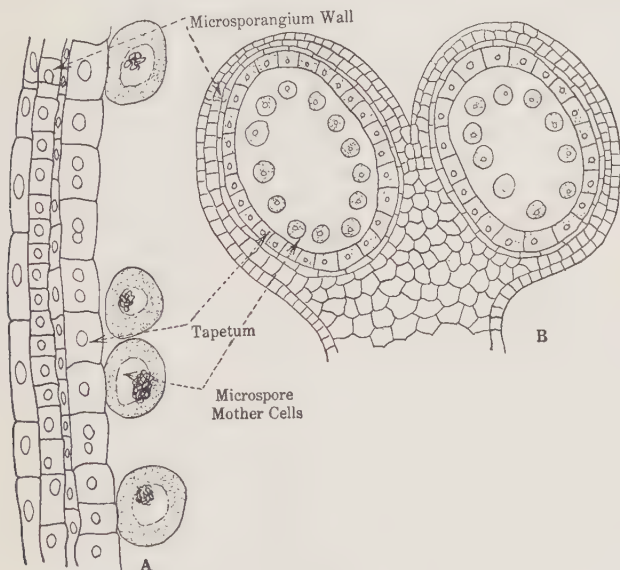


FIG. 227.—*A*, longitudinal section of a portion of the wall of the anther of wheat. *B*, transverse section of an anther lobe of wheat. (Redrawn from Percival.)

in groups of four. One of the last two divisions giving rise to these spores is a reduction division and reduces the chromosome number of the nuclei to the haploid number and thus the male gametophyte stage begins.

Megasporophylls and Megasporangia.—The megasporangium has its origin in a small mass of undifferentiated cells which protrude from the placenta. From the base of this projection arise two rings of tissue which grow up about the developing

megasporangium. These two layers of tissue (the integuments) finally entirely envelop the megasporangium proper, except for a small opening (micropyle) at the free end of the ovule.

While the megasporangium is still very small, one of the cells just below the epidermis of the nucellus becomes differentiated

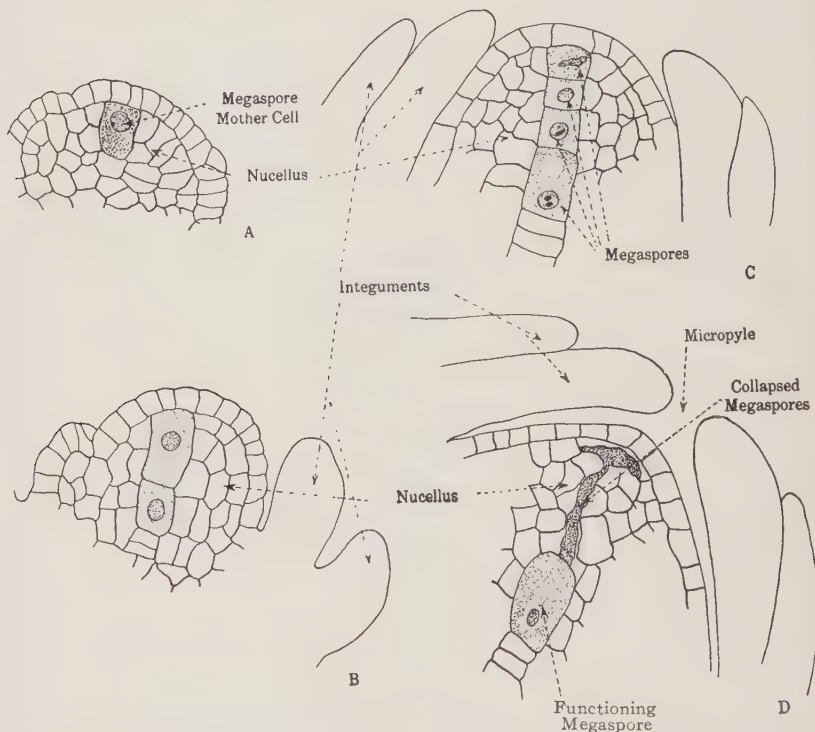


FIG. 228.—Median longitudinal sections of young ovules of wheat, showing development of the megaspores and the degeneration of all but one of these. (Redrawn from Percival.)

from the surrounding cells in size and in the appearance of its contents (Fig. 228 A).

The nucleus of this cell now undergoes two successive divisions one of which is a reduction division and reduces the chromo-

some number of the nuclei from $2x$ (the diploid number) to x (the haploid number) and thus initiates the female gametophyte stage of the life cycle. These divisions give rise to four potential megaspores (Fig. 228 *B* and *C*). These spores are not arranged in the characteristic tetrahedral groups, as are the spores of all Bryophyta and Pteridophyta and the microspores of seed plants, but in a straight row. Definite walls are formed around each megaspore. Soon the basal megaspore (the one farthest from the micropyle) begins to enlarge at the expense of the other three, and finally these three are completely absorbed, leaving a single large functioning megaspore, as in *Pinus* (Fig. 228 *D* and 230*A*).

The Male Gametophyte.—Germination of the microspore begins while it is still within the microsporangium. For convenience we shall consider the germination of the microspore and the development of the male gametophyte as taking place in the following stages:

1. Division of the protoplast of the microspore into a tube cell and a generative cell. The cytoplasm of these two cells is clearly differentiated, but they are not separated by a wall. (See Fig. 229.)

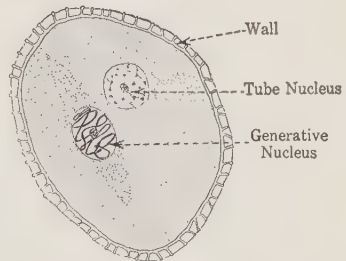


FIG. 229.—Pollen grain (microspore) of *Lilium* at the time of dehiscence of the anthers.

2. A little later, but, in wheat, before the shedding of the microspores, the generative cell divides to produce two male gametes. (In many angiosperms the second division does not take place until after the pollen tube is formed.)

3. Following pollination, the formation of the pollen tube.

4. Migration of the two male gametes into the pollen tube, and sometimes the migration of the tube nucleus as well.

The mature male gametophyte, consisting of three nuclei and some associated cytoplasm, is even more reduced than that of

Pinus, for in the latter case, in addition to the two sperm nuclei there are two vegetative cells, a tube cell, and a stalk cell. Compare Fig. 109.

The Female Gametophyte (Embryo Sac).—The protoplast of the megaspore now undergoes free nuclear division, as in *Pinus* and *Selaginella*. There results a female gametophyte consisting of eleven to fifteen nuclei lying free in a mass of vacuolate cytoplasm. In contrast with *Pinus* and *Selaginella*, in the angiosperms cell walls are not subsequently formed between the nuclei of the female gametophyte.

This process of development of the female gametophyte may be conveniently divided into the following stages (see Fig. 230):

1. **The first division of the megaspore nucleus results in two nuclei which promptly separate;** one of these moves to the micropylar end of the sac, and the other goes to the opposite (antipodal) end of the sac.

2. **Each of these two nuclei divides,** so that there are **two nuclei at the micropylar end, and two at the antipodal end.**

3. Following this second division, **each of the four nuclei divides,** resulting in eight nuclei, **four at the micropylar end and four at the antipodal end.**

4. Now, **a single nucleus from each group of four moves toward the center of the embryo sac.** The two nuclei (polar nuclei) lie in contact with one another without fusing until the time of fertilization.

5. **The three nuclei at the end opposite the micropyle divide, forming a group of six to eight antipodal nuclei.** Although not separated from one another by cell walls, each of these nuclei has about it a quantity of cytoplasm set off from that of neighboring nuclei, so that we may speak of them as cells (the antipodal cells). In most angiosperms there are only three antipodal cells.

6. Of the **three nuclei remaining at the micropylar end,** one is the **egg nucleus,** and the other two are the **synergid nuclei.** Each of these nuclei has associated with it a quantity of cytoplasm which is separated by a limiting membrane from the rest

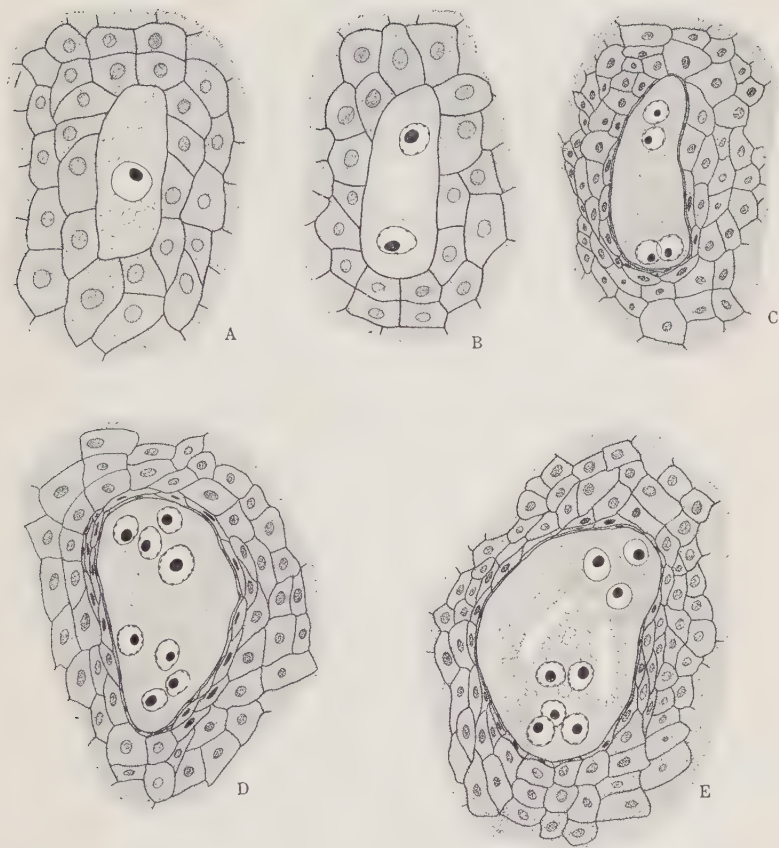


FIG. 230.—Stages in the development of the female gametophyte (embryo sac) of corn. Longitudinal sections. *A*, functioning megaspore, also spoken of as one-celled embryo sac. *B*, 2-celled embryo sac. *C*, 4-celled embryo sac. *D*, 8-celled embryo sac at time the polar nuclei have started to migrate. *E*, 8-celled embryo sac after the polar nuclei have migrated. The megaspore mother cell and embryo sacs are embedded in nucellar tissue. (Redrawn from Miller, in *Journal of Agricultural Research*.)

of the embryo sac. Thus at the time of fertilization the female gametophyte of wheat consists of (see Fig. 232 and compare Fig. 99):

(a) **Two synergids** or "helper cells" at the micropylar end of the embryo sac.

(b) **A single egg cell** near the synergids.

(c) **Two polar nuclei**, usually near the center of the embryo sac.

(d) **Six to ten antipodal cells**, at that end of the embryo sac which is opposite the synergids.

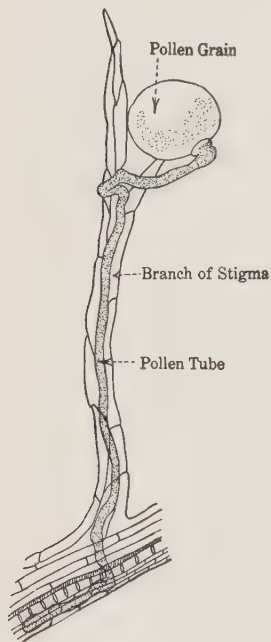


FIG. 231.—Single hair of the stigma of corn (*Zea mays*), showing path of the pollen tube. (Redrawn from Miller, in *Journal of Agricultural Research*.)

Pollination and Development of the Pollen Tube.—The pollen of wheat is carried to the plume-like stigma by the wind. Within an hour and a half to two hours after pollination the pollen tube begins to develop. (See Fig. 231.) It penetrates the tissue of the stigma and, entering the hollow style, grows downward into the ovary, where it finds its way to the micropyle. After passing through this opening, it penetrates the tissue of the nucellus and enters the embryo sac. (See Fig. 232.)

There is considerable variation in different angiosperms as to the length of the interval between pollination and fertilization. In wheat the union of the male gamete with the egg nucleus has been observed between thirty and forty hours after pollination. In most angiosperms the time interval between pollination and fertilization is from a few hours to several days, but there are species in which fertilization does not take place until eleven months after pollination.

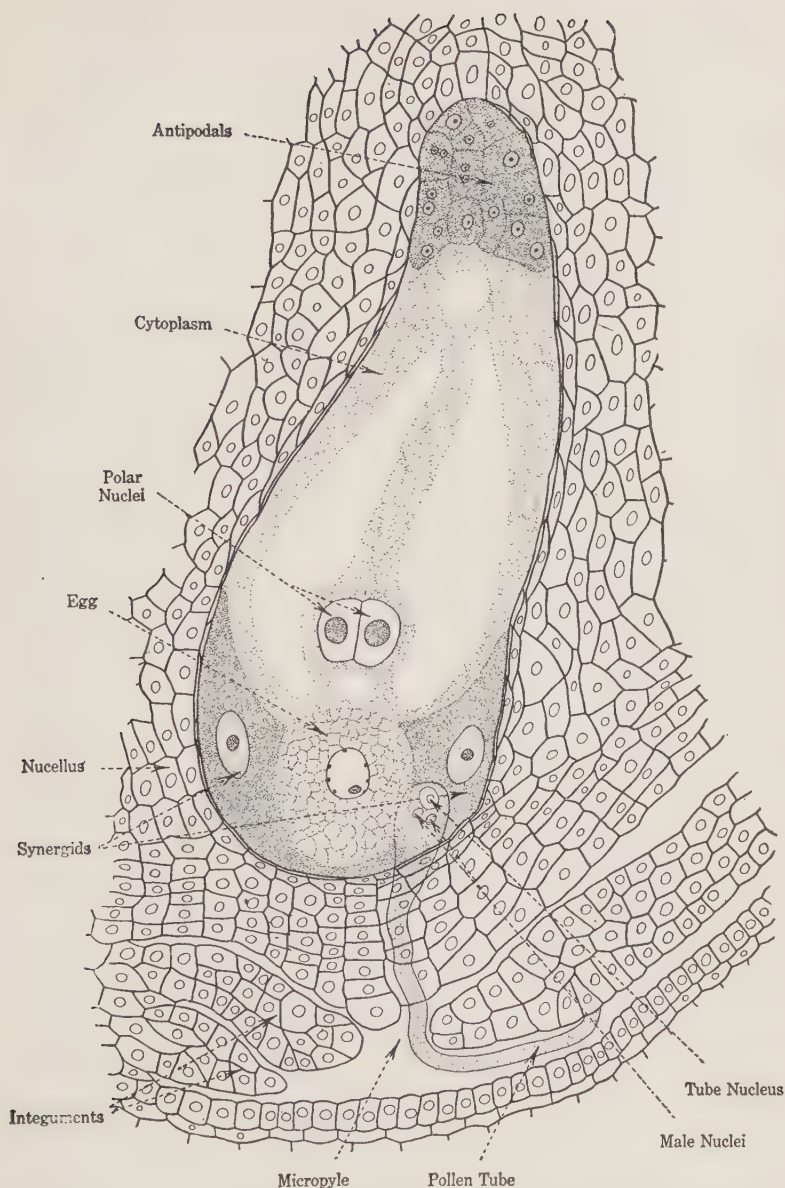


FIG. 232.—Longitudinal section of a mature embryo sac of corn (*Zea mays*) just prior to fertilization. (Redrawn from Miller in *Journal of Agricultural Research*.)
Essentially same as in wheat.

Fertilization.—After entering the embryo sac, the pollen tube grows toward the egg nucleus. The tip of the tube is then ruptured and its contents discharged. One of the sperm nuclei fuses with the egg nucleus to form the zygote nucleus, and the second sperm nucleus unites with the polar nuclei to form the primary endosperm nucleus. (See Fig. 233 and 234.)

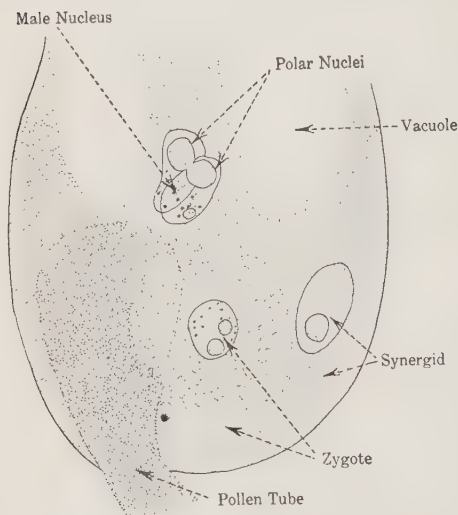


FIG. 233.—Longitudinal section of the lower portion of the embryo sac of corn at the time of fertilization. One male nucleus is shown fusing with the two polar nuclei, and the other male nucleus is shown fusing with the egg nucleus. (Redrawn from Miller, in the *Journal of Agricultural Research*.)

At the union of a sperm nucleus with the egg nucleus, the **resulting zygote marks the beginning of the new sporophyte generation.** The union of the second sperm nucleus with the two polar nuclei results in the formation of the **endosperm.**

By the union of the sperm with the egg, the zygote is furnished with one set of chromosomes from the male parent and another set from the female parent. Thus the zygote has the diploid chromosome number characteristic also of all the nuclei of the

sporophyte which develops from the zygote. These two sets are associated in all the cells of the sporophyte. That is, in the first division of the zygote nucleus and in all subsequent divisions of the sporophyte cells, chromosomes of paternal origin (contributed by the sperm nucleus) and those of maternal origin (contributed by the egg nucleus) split longitudinally and each daughter nucleus receives an equal amount of both maternal chromatin

and paternal chromatin. There is reason to believe that the chromatin contributed by the male and female gametes respectively maintains its individuality in the nuclei of all sporophyte cells. The basal megaspore begins to enlarge at the expense of the other three, and finally these three are completely absorbed, leaving a single functioning megaspore.

The synergids degenerate at about the time of fertilization. During the growth of the embryo and endosperm, the antipodal cells also slowly degenerate.

Development of Embryo Sporophyte.—The fertilized egg (zygote or oospore) becomes by repeated division a multicellular embryo sporophyte. In wheat the zygote undergoes division into two cells (this stage is not shown in the figures) a few hours after fertilization. The larger of these two cells is the suspensor and from the smaller cell the embryo develops. A

depression appears at one side of the embryo, marking the position of the growing point of the stem. The **scutellum** (single cotyledon) arises from the tissue above this depression. The origin and development of the other organs of the embryo are shown in Fig. 236.

It will be observed that in wheat the growing point has a lateral origin and the cotyledon is terminal in origin. This type of embryo development contrasts with that found in most

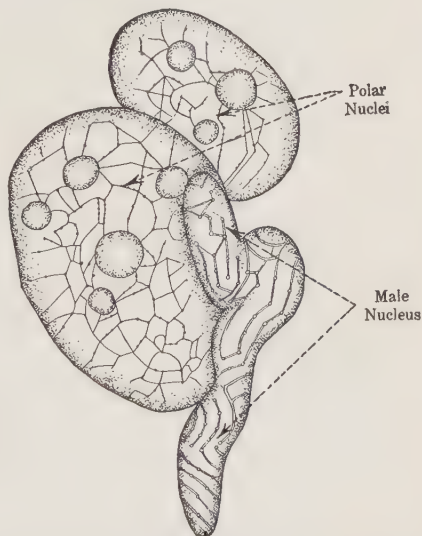


FIG. 234.—Fusion of male nucleus with two polar nuclei, in *Lilium aurantum*, to form the primary endosperm nucleus, $\times 1260$. (Redrawn from Blackman and Welsford.)

dicotyledons, as illustrated by *Capsella* (Fig. 110), in which the growing point is terminal in origin, and the cotyledons are lateral in origin.

In a comparison of the angiosperm embryo with that of the gymnosperm, pine, it is noted that in the latter the pro-embryo

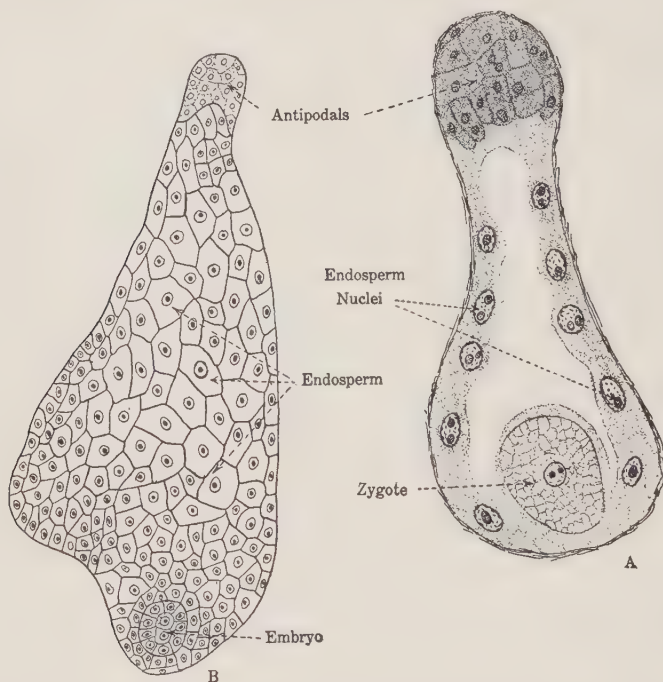


FIG. 235.—*A*, longitudinal section of the embryo sac of corn 12 hours after fertilization. *B*, 36 hours after fertilization. The magnification of *A* is more than twice that of *B*. (After Miller, in *Journal of Agricultural Research*.)

consists of a group of sixteen cells, in which the suspensor becomes a much elongated structure pushing four cells of the pro-embryo deep down into the endosperm, where each develops into an embryo.

Development of the Endosperm.—In *Pinus* and in most other gymnosperms the nutritive tissue of the seed, the endosperm

is the female gametophyte, a mass of tissue developed by repeated divisions of the megaspore. Even at the time of fertilization, this gametophyte tissue makes up, in *Pinus*, a considerable part of the ovule, and after fertilization it continues to grow until it finally displaces all the tissue of the nucellus. In wheat and all other angiosperms the endosperm has an entirely different origin. It is initiated, not by the germination of the megaspore, as in

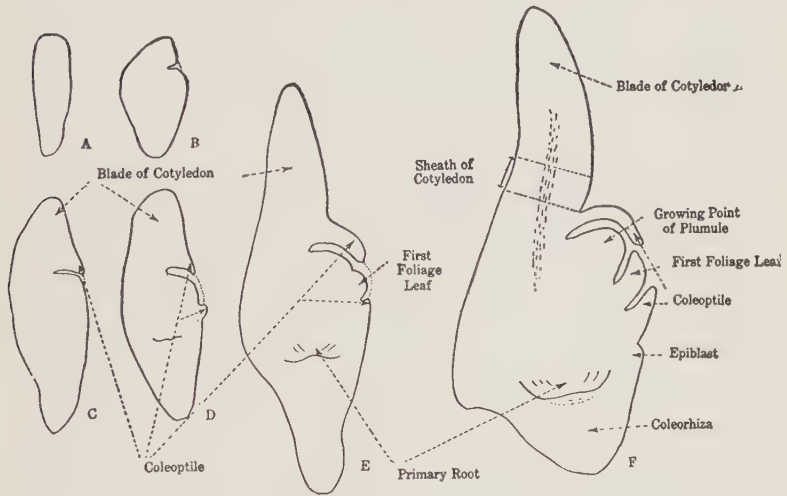


FIG. 236.—Longitudinal sections of embryos of wheat in various stages of development. (Redrawn from Percival.)

Pinus, but by the division of the primary endosperm nucleus of the fertilized embryo sac.

Although the first division of the zygote is followed by wall formation and all the cells of the embryo are enclosed in cell walls, the endosperm develops at first by free nuclear division (Fig. 235 A), that is, repeated division of nuclei without cell wall formation. This process has already been met with in the development of the female gametophytes of *Selaginella* and *Pinus*. In wheat walls are later formed about the free nuclei, and a more

or less compact endosperm tissue results (Fig. 235 *B*), the cells of which are largely filled with starch and protein.

It will be recalled that in many plants, such as peas, beans, alfalfa, squash, and sunflower, the endosperm is completely

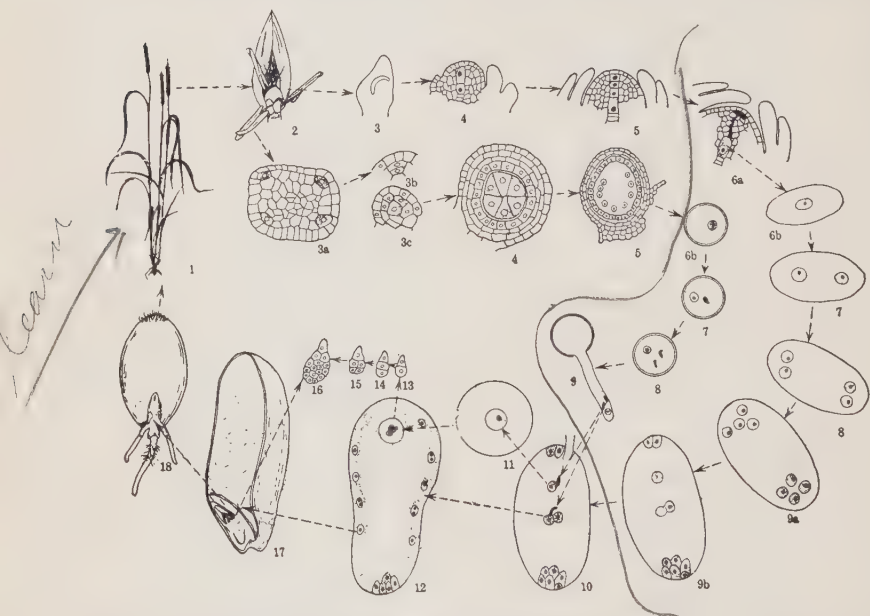


FIG. 237.—Diagrams showing stages in the life cycle of wheat. 1, mature sporophyte; 2, single flower; (outer circle) 3, 4, 5 and 6a and 6b, stages in the development of the megaspore; (inner circle) 3a, 3b, 3c, 4, 5, and 6b, stages in the development of the microspore; (outer circle) 7, 8, 9a and 9b, stages in the development of the female gametophyte; (inner circle) 7, 8 and 9, development of the male gametophyte and germination of pollen grain; 10, process of double fertilization; 11, zygote; 12, developing zygote and endosperm within the embryo sac; 13, 14, 15, 16, early stages in the development of the embryo sporophyte; 17, mature grain in longitudinal section showing mature embryo and endosperm (dotted); 18, germinating embryo.

absent in the mature seed due to its absorption by the developing embryo previous to the maturing of the seed. In wheat, as in all other grasses, and in the castor-oil plant, and many other angiosperms, the endosperm constitutes a large part

of the mature seed, performing its function of supplying food to the embryo after germination begins, not before the seed matures.

The Seed.—In the enlargement of the embryo and endosperm, the tissue of the nucellus is encroached upon and either partially or totally absorbed. In the mature wheat seed the nucellus constitutes a thin layer of cells, covering the outer surface of the endosperm. In the young wheat seed there are also two integuments, each consisting of two layers of cells. In the maturing of the seed the outer integument is entirely absorbed, so that the mature seed coat has but two rows of cells belonging to the inner integument. It will be recalled that the so-called “seed” or grain of wheat is in reality a one-seeded fruit, in which the ovary wall has become firmly attached to the ovule.

Thus, as a result of nuclear fusions in the embryo sac, which is embedded in the megasporangium (nucellus of the ovule), there follows a series of changes, involving all the tissues of the ovule, which result in a structure termed the seed. The mature wheat seed possesses tissue belonging to (1) the **parent sporophyte**, (2) the **embryo sporophyte**, and (3) also an **endosperm**, which cannot properly be designated either as sporophytic or gametophytic. The seed coats and the nucellus belong to the parent sporophyte.

Important Points of Contrast between Gymnosperms and Angiosperms.—

1. The seeds of gymnosperms are borne upon the surface of the megasporophylls, while the seeds of angiosperms are always formed within a closed structure, the ovary, formed by the union of the margins of one or more megasporophylls (carpels).

2. Gymnosperms are all woody, perennial forms, and with few exceptions are evergreen. Angiosperms include both herbaceous and woody plants, and annual, biennial and perennial forms.

3. In all gymnosperms, except the *Gnetales*, tracheal tubes are lacking, whereas in almost all angiosperms the xylem has tracheal tubes.

4. In gymnosperms the pollen comes into direct contact with the nucellus of the megasporangium, whereas in angiosperms the pollen comes in contact with the stigma, the tip of a structure (the pistil) consisting of one or more megasporophylls (carpels), which enclose the megasporangia.

5. In contrast to gymnosperms, angiosperms usually have sepals and petals associated with the megasporophylls and microsporophylls, the whole forming a characteristic structure called the flower.

6. In gymnosperms the first divisions of the zygote result in a number of free nuclei; in angiosperms such free nuclear division of the zygote does not occur.

7. The male gametophyte of gymnosperms consists of six cells; whereas that of angiosperms is somewhat more reduced, consisting of but three cells.

8. The female gametophyte of gymnosperms is an extensive tissue consisting of many thousands of cells separated by walls and giving rise to archegonia. The female gametophyte of angiosperms is usually an eight nucleate structure (embryo sac), generally without separating cell walls, which never develops archegonia.

9. The more primitive gymnosperms produce motile male gametes; such gametes are not formed in any angiosperms.

10. In the gymnosperm embryo there are normally three to eight cotyledons; in angiosperms either one (in the monocotyledons) or two (in the dicotyledons) is the rule.

CHAPTER XV

EVOLUTION AND HEREDITY

Evolution.—It has long been held by those best acquainted with plants and animals that all the thousands of species of organisms which exist to-day, or have existed in the past, have originated from previously existing species and that they all therefore have arisen by the process we call evolution from one or a few original kinds.

We shall attempt in this chapter to summarize, in so far as is possible in a few pages, the principal theories as to the method of evolution and some of the most important facts bearing upon these theories.

Heredity and Variation.—There are two remarkable tendencies which are characteristic of all organisms. These two tendencies are **heredity** and **variation**. Heredity may be defined as the tendency of the progeny to be like the parents and therefore to resemble each other. Variation, on the other hand, is the tendency of the progeny to differ from the parents and from each other. It is clear that without variation no new species could ever have arisen from pre-existing species.

That like begets like is one of the most obvious facts in human experience. Even primitive peoples recognize the fact that characteristics are passed on from parents to children and that acorns, the seed of oaks, always grow into oaks and never into pines or apple trees.

However, it is literally true that no two individuals of a species are exactly alike. The familiar expression "as like as two peas in a pod" which is so commonly used to indicate the closest of resemblances, directs the attention of the individual to an excel-

lent example of the dissimilarity (variation) which we find among all plants and animals, for actually no two peas are alike. In fact, every pea in a pod, and even every pea on a plant is different from every other, and the plants which would develop from these peas, if they germinated, would all show differences in such particulars (**characters**) as size and form of the root system and of the shoot, branching, form, size and arrangement of the leaves, size and arrangement of the flowers, and many other characters.

The question is immediately suggested: Why do the progeny tend to be like the parents and why are they often quite unlike and always slightly different from the parents? The cause can be stated more briefly and simply in the case of heredity than in that of variation. The progeny generally closely resemble the parents because their living substance was derived from the parents. If the new individuals have arisen by vegetative methods, as in the case of stem cuttings and bulb formation, it is clear that all the protoplasm of the new plant came originally from the single parent. In sexual reproduction the new individual develops from a fusion cell or zygote in which are combined a protoplast from one parent with a protoplast, or at least a nucleus, from the other parent. In either case there is continuity of living material from parent to progeny and the tendency to likeness must be due to this continuity. The fact that in many seed plants only the nucleus, and apparently none of the cytoplasm of the male gamete, fuses with the egg cell, indicates that at least in these cases it is principally the nuclei which transmit the characters of the parents to the new individual.

Chromosome Theory of Inheritance.—According to this theory it is the chromatin (the material of the chromatin granules in the resting nuclei and of the chromosomes in dividing nuclei) which bears the inherited characters. The number of chromosomes is constant for each species, except, of course, for the fact that the number is doubled at fertilization and halved again at the reduction division. There is very good reason to believe that

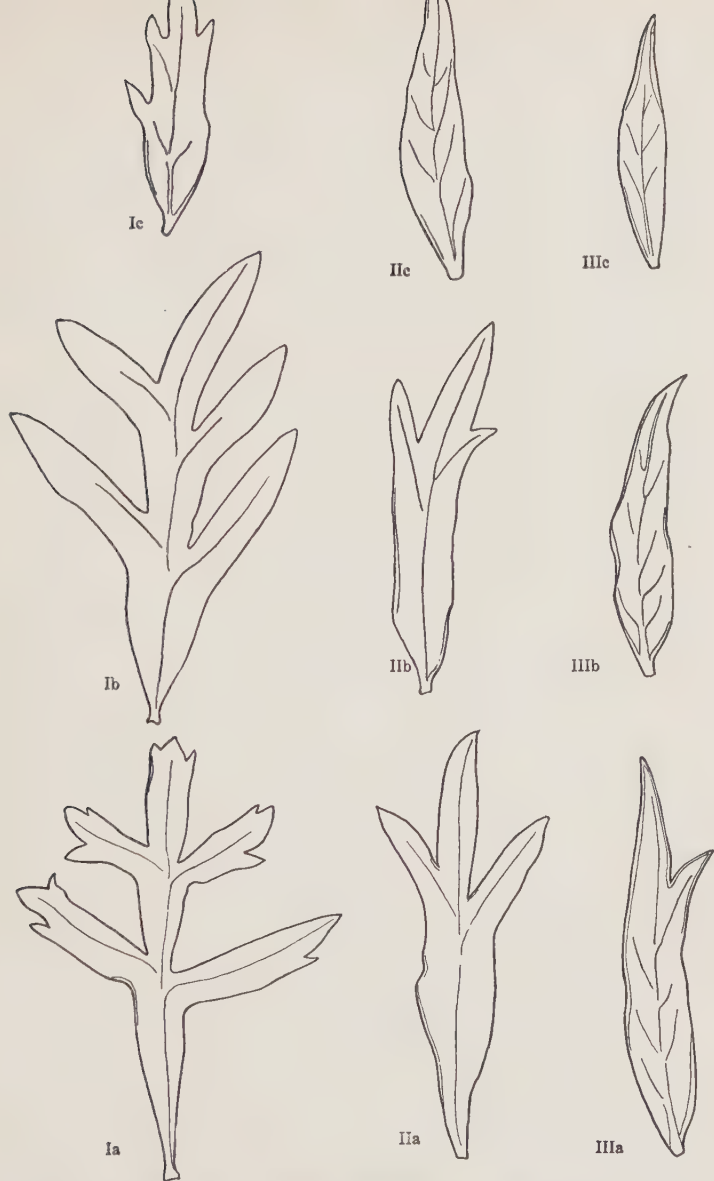


FIG. 238.—Leaf variations in *Artemisia vulgaris*. The leaves in each vertical row are from a single plant and thus show variation in one individual. Thus 1a is from near the base of a given plant, 1b from about half way up the stem of that plant and 1c from near the tip of the same plant. The leaves in each horizontal row are from corresponding parts of three different plants and thus show variations between different individuals. (Redrawn from Clements and Hall's *The Phylogenetic Method in Taxonomy*.)

the identity of these chromosomes is not lost in the period between nuclear divisions, even when they break up into chromatin granules and remain in that condition in the resting nucleus. It is quite certain that with rare exceptions inheritance is due to the continuity of chromatin from one generation to another.

Kinds of Variations.—We recognize three principal kinds of variations in plants:

(a) *Modifications.*—These are minor individual variations which are largely due to differences in the soil, moisture, light or other environmental conditions. If, for example, we planted the seeds from a single self-fertilized wheat plant, the progeny might vary considerable in height of plant, length of heads, and other characters. Such variations, *in as far as they are the result of differences in the environment of the different plants* are called **modifications**, and variations of this type are probably not inherited.

(b) *Mutations.*—Practical growers have observed from time to time that, among hundreds of thousands of plants of a given strain, there sometimes appear individuals with characters markedly different from those of the general "population" and which breed true for the characters in question. Variations of this kind are called **mutations**, and are popularly known as "sports." As already mentioned, such variations are inherited, presumably because some change in the chromatin has accompanied their appearance, whereas modifications are not inherited and probably are not connected with any change in the chromatin of the nuclei. The red sunflower, the bush Lima bean and the Concord grape are examples of mutations. No doubt there appear from time to time in many of our fields of cultivated plants, such new forms, that is mutations, and if we have an eye trained to distinguish such forms we may be able to discover a valuable mutation which can then be propagated and grown in large quantities.

Sometimes bud mutations or bud sports occur. Thus there may occur on a fruit tree a single branch (developed of course from a single axillary bud) which bears fruit differing in some particular from the other fruit on the tree. If the qualities of

the fruit of this "bud mutant" branch are desirable, buds may be taken from the branch and used for budding, thus multiplying the bud mutation. In this connection it should be borne in mind that the bud mutation arises with the formation of a lateral bud, presumably through some change in the chromatin when this bud originated from the premeristem. The whole branch developing from the mutant bud has the characters of the bud sport. Certain varieties of the navel orange and of the Boston fern are examples of bud mutations.

(c) *Combinations*.—When plants belonging to two different varieties or species are crossed new variations arise as the result of the combination of the different characters of the parents. Variations of this type are spoken of as **combinations**, and they will be discussed in more detail in the following paragraphs.

Mendelian Inheritance.—A large part of the work which is being done to-day on the experimental study of evolution, as well as of the practical work of the plant and animal breeder, is largely based upon the remarkable discoveries of the Austrian monk, Gregor Johann Mendel. His experiments had to do with the manner of inheritance of certain characters by the individuals resulting from the crossing or hybridizing of two organisms differing in one or more characters. He worked for the most part with the garden pea (*Pisum sativum*).

His discoveries, the outcome of eight years of breeding experiments, were published in an obscure scientific periodical in 1866. Partly on that account and partly because the time was not yet ripe for a proper appreciation of its significance, his work remained practically buried for thirty-five years. In 1900, sixteen years after Mendel's death, his publication was discovered almost simultaneously by three botanists, who had been led by their own studies to conclusions similar to his.

His first experiments were made by crossing two varieties of garden peas, a dwarf variety (20–45 centimeters high) and a tall variety (175–200 centimeters high). That is to say, he grew plants of these two varieties and used the pollen from each to

pollinate the flowers of the other variety. Peas were favorable plants for his study because the pea is a species which is naturally self-fertilized. On that account, it was reasonably certain, since the seeds produced naturally by the tall variety and the dwarf variety always produced plants which were respectively tall and dwarf, that the varieties were pure as regards tallness and dwarfness.

Mendel found that, whether he used pollen from a dwarf plant to pollinate the stigma of a tall plant or vice versa, the seeds formed gave on germination only tall plants. In different form, these results may be stated thus: When the dwarf variety was crossed with the tall variety all of the individuals of the first (**hybrid**) generation commonly spoken of as the F_1 (or **first filial**) generation, were tall.

In the F_2 (**second filial**) generation, secured by allowing F_1 individuals to self-pollinate, about one-quarter of the individuals were dwarf and about three-quarters tall. Mendel secured 787 tall to 277 dwarf plants. When the F_2 dwarf plants were self-pollinated, all their progeny were dwarf plants. These dwarf F_2 and F_3 plants were like the dwarf plants which were crossed with the tall plants at the beginning of the experiments and they never gave any tall plants as long as they were bred with dwarf plants. Two-thirds of the tall plants of the F_2 generation (that is, one-half of all the F_2 individuals) when self-pollinated, gave one-quarter dwarf and three-quarters tall plants. (See Fig. 239.) The remaining tall F_2 plants, when self-pollinated, gave nothing but tall plants, which in turn gave nothing but tall plants when self-pollinated. In short, although the F_2 plants appeared to be only of two kinds, dwarf plants and tall plants, there were actually three kinds of F_2 plants.

(1) Dwarf plants (about one-quarter of all) which gave only dwarf plants when self-pollinated.

(2) Tall plants (about one-half of all the F_2 plants) which when self-pollinated, gave one-quarter dwarf and three-quarters tall plants.

(3) Tall plants (about one-quarter of all of the F_2 plants and

in appearance like the other tall plants) which gave only tall plants when self-pollinated.

For these three kinds of plants it is convenient to use the following designations, the meaning of which will shortly be made clear:

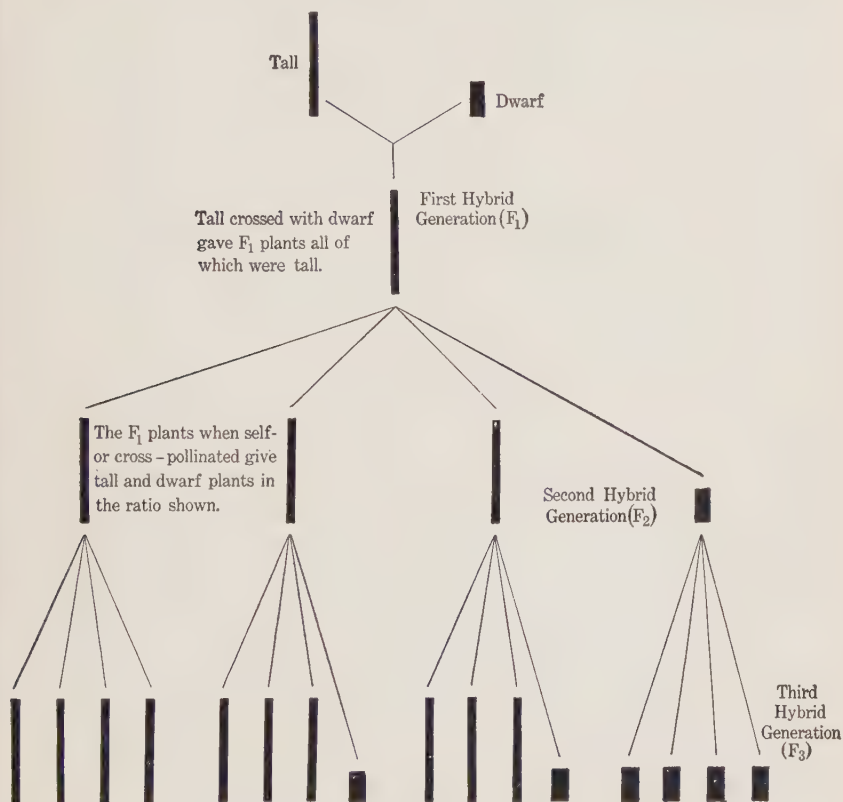


FIG. 239.—Diagram to illustrate inheritance in a monohybrid cross between tall and dwarf peas.

(1) **Pure recessives**, (2) **Hybrids**, and (3) **Pure dominants**.

It is important to bear in mind that the pure recessives, when self-pollinated or cross-pollinated among themselves, never gave anything but pure recessives, in this case dwarf plants; that

the hybrids, when self-pollinated or crossed among themselves, gave the three classes in the proportion 1 : 2 : 1; and that the pure dominants, when self-pollinated or crossed among themselves, gave only pure dominants.

Mendel secured results like those just described when he crossed pea varieties having smooth and wrinkled seed coats, and when he used still other varieties characterized by green and yellow cotyledons.

Such characters as those of tallness and of dwarfness in Mendel's peas, when inherited, remain distinct and are thus transmitted as integral units. From the fact that the tall F_1 plants gave some dwarfs when self-pollinated, it is clear that the character for dwarfness was transmitted through the tall F_1 plants as a unit which was not affected by its association with the character for tallness.

One of the most remarkable facts about Mendel's breeding experiments with tall and dwarf peas is that although the F_1 plants had received both the character for dwarfness and the character for tallness, the plants were actually tall; that is to say, the character for tallness prevented the opposite character from coming to expression. On this account the character for tallness is spoken of as a **dominant character**, and that for dwarfness as a **recessive character**. This prevention of the expression of a recessive character by a dominant character does not always occur in Mendelian inheritance. For instance, when the red-flowered variety of the common garden four o'clock is crossed with the white-flowered variety, the F_1 plants are pink, neither color being dominant.

Explanation of Mendel's Results on the Basis of Chromosome Behavior.—It will be recalled that, with a few exceptions, inherited characters are transmitted from one generation to the next through the chromosomes. That is to say, the progeny have a certain character which was possessed by one or both parents because the nuclei of the new plants contain chromosomes received from the parents. In at least one of the chromosomes

of the gametes of each of the original dwarf and tall plants there was a definite and fixed part, or factor, which was the carrier of the character "tallness," in the tall plants, and of the character "dwarfness," in the dwarf plants. Similarly for every other character there was present in the gametes at least one factor in some one of the chromosomes. Now when fusion of gametes (egg and sperm) takes place the diploid nucleus of the zygote will have at least two chromosomes with a factor influencing



FIG. 240.—Chromosome individuality as shown in *Crepis capillaris* (left) and *C. scotosa* (right). The two chromosomes connected by dotted lines to a single Roman numeral are homologous. Each of the chromosomes has already begun to split since the stage of mitosis shown is the metaphase of somatic (2x) nuclei. The chromosomes are shown as seen from a point on the axis of the spindle. Note the similarity in size and form of the two chromosomes in each homologous pair. The use of the same numerals in the left-hand and the right-hand part of the figure is not meant to indicate corresponding chromosomes. Compare text, page 753. (From Collins and Mann, in *Genetics in Relation to Agriculture* by Babcock and Clausen, McGraw-Hill Book Co.)

stature, one from the egg and one from the sperm. Such a pair of chromosomes coming respectively from sperm and egg and each with a factor influencing the same kind of character is called a pair of *homologous chromosomes*.

Now the original dwarf plants which Mendel used for his experiments had in their nuclei no chromosome with a factor for tallness. That is to say, these plants were **homozygous** for this

character, "dwarfness." Accordingly when they were self-pollinated both the chromosomes of the homologous pair affecting stature had the factor for "dwarfness."

The original tall plants were also homozygous because their nuclei contained no chromosomes with a factor for dwarfness but two homologous chromosomes bearing the factor for tallness. Since these plants are naturally self-fertilized, there is little possibility, under normal conditions, of the introduction of a chromosome with the factor for tallness into the nuclei of the progeny of dwarf plants. Accordingly they produce only dwarf plants (i.e., "breed true"). For the same reason, the original tall plants would also breed true under normal conditions.

In the reduction division, a little before the formation of microspores (pollen grains) and megaspores (one of which gives rise to the embryo sac), the members of each pair of homologous chromosomes are separated from each other and pass to opposite ends of the spindle. Accordingly, the megaspores and microspores (and the same is true of the sperm nuclei and egg nucleus), each contain only one chromosome from each pair existing in the sporophyte nuclei. Since, in the dwarf plants, both the chromosomes of the homologous pair carrying the factors for stature in the sporophyte carry the factor for dwarfness, the egg nuclei and the sperm nuclei are all alike with respect to the factors for statures. Similarly, all the sperm nuclei and egg nuclei produced by the tall plants are alike in that they have the factor for tallness only.

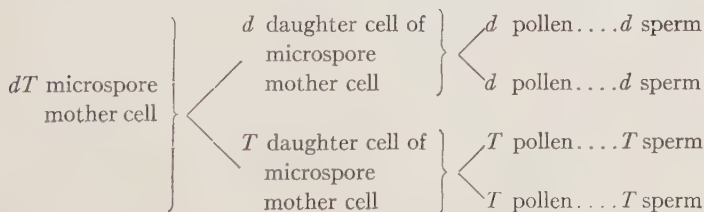
It will make the rest of our explanation somewhat easier to grasp if we substitute the capital letter T for the expression "factor for tallness," and the small letter d for the expression "factor for dwarfness," the capital letter indicating that the corresponding character is dominant, and the small letter that the corresponding character which it represents is recessive. It will also be convenient to designate the gametes bearing one of these factors as T sperm, T egg, d sperm and d egg, and the zygotes resulting from their fusion as dT zygotes, dd zygotes and TT zygotes.

The fact already stated, that Mendel's original dwarf plants bred true, can be restated thus, using the designations just mentioned. *Since, in the case of the sporophytes of the dwarf, both members of the pair of homologous chromosomes controlling stature bear the factor for dwarfness, only d sperms and d eggs will be produced by the dwarf plants when self-pollinated or crossed with other dwarf plants. Therefore all the zygotes which are formed by the fusion of these gametes will be dd zygotes and will give rise to dwarf plants.*

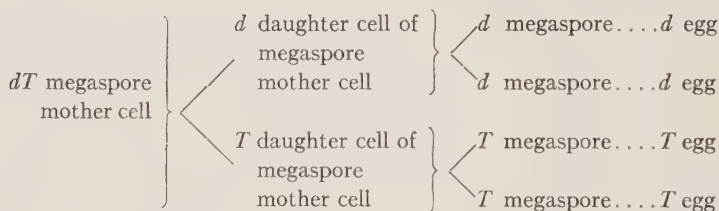
As stated in earlier chapters, the double number of chromosomes in the zygote of any plant consists of pairs of homologous chromosomes, one chromosome of each pair having come from the sperm and one from the egg cell.

The F_1 Generation.—Now when dwarf and tall plants are crossed, pollen from the dwarf variety may be used to pollinate pistils of the tall variety, in which case d sperm $\times$ T egg = dT zygote; or pollen from the tall variety may be used to pollinate flowers of the dwarf variety, in which case T sperm $\times$ d egg = dT zygote.

In both cases the zygote contains a pair of homologous chromosomes, each of the members of which bears one of the contrasting factors. Accordingly the F_1 plants developed from these zygotes will be **heterozygous**, and on account of the dominance of the tall character will be tall plants. Now at the reduction division of the microspore mother cell, the d chromosome and the T chromosome, which have been associated as homologous chromosomes in all the nuclei of the sporophyte plants, are separated thus:



As a result, the pollen grains and the sperm cells are of two kinds, T and d , produced in equal numbers. Similarly there are produced T eggs and d eggs in equal numbers, as is shown in the following diagram:



As pointed out on page 331, three of the megaspores are completely absorbed, leaving a single functioning megaspore. In half the cases the functionary megaspore will be a d megaspore and in half the cases a T megaspore, so that the numbers of d and T eggs in the ovaries of the F_1 plants will be approximately the same.

Such separation at the time of the reduction division of the two members of a pair of homologous chromosomes bearing contrasting characters or **allelomorphs**, so that half of the gametes have the factor for one character and half the factor for the other character, is spoken of as **segregation**. The resulting **purity of the gametes** is one of the most important features of Mendelian inheritance.

The F_2 Generation.—Now when an F_1 plant is self-pollinated or cross-pollinated with other F_1 plants, there will be four possible combinations of sperm and egg, since there are two kinds of sperms and two kinds of eggs; and these combinations, by the law of probability, will occur in about equal proportions. These combinations are:

- (1) T sperm $\times$ T egg giving TT zygote,
- (2) d egg $\times$ T sperm giving dT zygote,
- (3) T egg $\times$ d sperm giving Td zygotes, and
- (4) d sperm $\times$ d egg giving dd zygotes.

These four combinations and their origin may be shown graphically by the following checkerboard diagram. In this the two kinds of sperms are placed in the horizontal row, the two kinds of eggs in the vertical row, and the possible combinations of gametes are shown in the four squares:

	<i>T</i> <i>d</i> sperms	
<i>T</i>	1 <i>TT</i>	3 <i>Td</i>
	2 <i>dT</i>	4 <i>dd</i>
<i>d</i>		

eggs

Let us consider briefly the result of these four combinations as they are expressed in the individuals of the F_2 generation. Combinations 2 and 3 are identical, since in both there is a

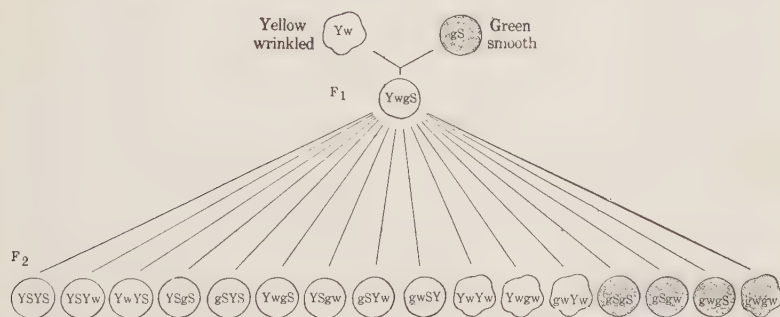


FIG. 241.—Diagram to illustrate inheritance in a dihybrid cross between a pea which would have produced yellow wrinkled seeds if self pollinated and one which would have produced green smooth seeds if self pollinated. Wrinkled seeds are distinguished from smooth by their outline and green from yellow by shading of the former. The letters show the various combinations of factors.

chromosome bearing the factor for dwarfness and a chromosome with the factor for tallness. Together, these zygotes will make up half of all the zygotes resulting from the cross. They will

all form seed which will develop into tall plants on account of the dominance of tallness. In fact, these plants are the ones which we designated earlier as the **hybrid**, F_2 plants. (See pages 349 and 350.) They are identical with the F_1 plants in appearance and in their behavior when interbred, i.e., self-pollinated or pollinated with pollen from similar plants.

The zygotes resulting from combination 4 will develop into **homozygous** plants for this character, since in this case both the members of the pair of homologous chromosomes governing stature bear the same factor (dwarfness). They will be dwarf plants, since the dominant character is entirely absent, and on the same account tall plants can never arise from them as long as they are interbred. These are the plants which were designated in an earlier paragraph (pages 349 and 350) as **pure recessive plants**. They are indistinguishable in appearance, and in their behavior when interbred, from the original dwarf plants used at the beginning of the experiment.

The zygotes resulting from combination 1 will be homozygous also, and will correspond in their behavior with the pure recessive, except that they and their progeny will all be tall plants instead of dwarf. They are the plants that were spoken of in an earlier paragraph as the **pure dominants** and are indistinguishable from the original tall plants used at the beginning of the experiment.

Theories as to the Origin of Species.—Direct Response to Environment.—According to the theory of Geoffroy St. Hilaire, the French naturalist (1772-1844), new species have arisen in direct response to changes in the environment. That is to say, as climatic and other conditions on the surface of the earth have slowly altered, these changes have called forth variations in the organism. A succession of such variations in a species might result in a new species. St. Hilaire believed some of these changes to have been favorable, or at least not unfavorable, and that the individuals which underwent these changes survived. Others were unfavorable and resulted in the destruction of the individuals.

Use and Disuse.—Jean de Lamarck, another French naturalist, proposed an explanation of evolution which is commonly spoken of as the theory of “use and disuse.” It is a familiar fact that, in the case of individuals, the continued use of a part of the body, as, for instance the muscles of the arm of a blacksmith, results in a development of that organ which makes it better able to do the work habitually required of it. It is also true that persistent disuse of an organ is apt to result in its partial degeneration or even suppression. Now Lamarck believed that changes in the environment might bring certain organs into disuse and increase the extent to which other organs were used, and thus bring about degeneration of certain organs and build up or modify others. Moreover, he regarded these characters acquired during the life of an individual as heritable. Thus the environment might, by reduction or suppression of certain organs and development of others, cause new species to arise.

Lamarck's theory was founded on three assumptions: (1) that the environment changes, (2) that use and disuse may alter the character of an individual, and (3) that the variations thus acquired can be inherited. The first two assumptions are recognized as correct, but there is no convincing evidence to indicate that acquired characters (modifications) can be inherited.

Orthogenesis.—Another theory, which has been advanced by different men and in different forms, is that there is inherent in every species a tendency to vary in a certain definite direction. If variation in this direction does not result in the individuals becoming less favorably adapted to their environment, new species will arise and these in turn will give rise to others. Otherwise the variations will not persist. The principal objections to this theory are as follows: (1) It has never been shown that such a persistent tendency to vary in a certain direction exists. (2) No explanation has ever been given as to the driving force or principle which is responsible for the assumed tendency.

Darwin's Theory of Natural Selection.—The most famous of the theories of evolution is Charles Darwin's theory of natural selection. The principal features of this theory are as follows:

1. Plants and animals in nature produce many more progeny than can possibly survive.

2. On account of this production of individuals far beyond the earth's facilities to support them there is a struggle for existence.

3. Individual organisms differ in their fitness for a given environment.

4. Through the struggle for existence there is a natural selection which results in the survival of the fittest or, to put it conversely, in the destruction of the unfit.

5. The individuals of a species are not all alike and even among the progeny of the same parents there are always at least slight variations.

Illustrations of the kind of variations which, according to Darwin, provide the material for natural selection can be secured by measurements of any plant or animal structure in many individuals of a given species. Thus if the length of all the bean seed in a lot is measured, and if all those having approximately the same length be sorted out, the following relation will be found to exist: The number of the beans having the least length will be very few. Those having the greatest length will also be very few. Between these extremes the numbers will increase as we approach the length halfway between the two extremes, or at near which we will find the largest number of individuals. The variations in question are often spoken of as fluctuating variations and probably include cases of the nature of both modifications and combinations. If the variations can be inherited it is possible, by selecting through some generations, to increase the average length of the beans. Thus the length characteristic of the greatest number of beans in any generation would be displaced in the direction of the extreme length. There is no reason, however, for believing that the extremes would change. Instead,

the greatest length and the shortest length would remain the same, and unless the extremes of variations can be shown to be changed by selection nothing new has been produced. The mere increase in the relative number of individuals varying in a given degree, which degree of variation already existed, cannot account for the origin of a new species. In short, there is some question whether natural selection of fluctuating variations can push the range of variation beyond certain limits which are characteristic of a species.

Another objection to Darwin's theory of the origin of new species is that the variations involved seem for the most part to be too small to be of life and death importance to the organism and to be the basis of natural selection.

The Mutation Theory of Evolution.—Hugo De Vries, the great Dutch student of mutation, suggests that new forms originate by mutation rather than by fluctuating variations. The principal features of the mutation theory of evolution are the following: (1) There arise from time to time, among the individuals of a species, forms which differ relatively widely in one or more characters from typical individuals. (2) The characters of these variations (mutations) are inherited, at least in many cases. (3) These mutations arise quite independently of fluctuating variations. (4) Mutations may take place in any direction. (5) The **mutants** (mutating individuals), at least in many cases, differ sufficiently from typical plants to make them subject to natural selection. (6) Accordingly, in nature all unfit mutants are likely to be eliminated by natural selection.

The uncertainty which exists as to the method by which new species arise is not to be interpreted as indicating any serious doubt on the part of biologists that new species do arise by natural processes; in other words, that evolution does take place, although how it operates is not yet entirely clear.

INDEX

(An asterisk (*) indicates an illustration.)

A

- Abies*, 309
- Absciss layer, *116
- Absorption, 1, 25
 - of inorganic salts, 96
 - of spectrum, *120
 - of water, 93
- Acer*, accessory buds of, 8
 - samara of, *157
 - winged fruit of, *169
- Acetic acid fermentation, 235
- Acorn, of oak, *159
- Active buds, 9
- Adventitious buds, 8
- Adventitious roots, 80
- Aecidia, on barberry leaf, *265, 267
- Aecidiospores, *262, 267
- Aecidium, *262
- Aerial stems, 12
- Aesculus*, twigs of, *44
- After-ripening, 177
- Agaricus campestris*, 269
- Aggregate fruit, *157
- Air, in the soil, 187
 - movements, as affecting rate of transpiration, 127
 - temperature, as affecting rate of transpiration, 127
- Akene, *159
- Albugo candida*, 244, *245, *246, *247
- Alcoholic fermentation, 234
- Algae, 203
 - blue-green, 207
 - brown, 207
 - characteristics of, 206
- Algae, classes of, 207
 - green, 207, 211
 - red, 207, 226
 - relative complexity of, 227
- Algal fungi, 229
- Alkali soil, 188
- Allelomorphs, 354
- Alternate buds, 8
- Alternation of generations, in Bryophyta, 272
 - in Phaeophyceae, 224
- Aluminum, 195
- Amanita*, 269
- Amino-acids, 173
- Amylase, 173
- Anagallis*, sessile leaf of, *101
- Anatomy, 2
 - of leaf, 105
- Anchorage, 97
 - by roots, 5
- Androsporangia, in *Oedogonium*, *218
- Angiospermae, 45, 46, 309
 - and gymnospermae, a comparison, 326, 341
- Angiosperms and gymnosperms, points contrast, 326, 341
- Animals, as agency in disseminating seeds, 168
- Annual, 15
 - winter, 15
- Annual rings, *47, *48, *49, 50
- Annular tracheal tube, *53, *69
- Annulus of fern sporangium, *296
- Anther, 134, *135, *136, 138
 - of lily, *138

- Anther, of wheat, development of, *328, *329
- Antheridia, of *Albugo*, 244
 of fern, *294
 of *Fucus*, *224
 of *Funaria*, *281
 of *Marchantia*, *278
 of *Oedogonium*, *217, *218
 of *Riccia*, *274
 of *Saprolegnia*, *244
 of *Selaginella*, 301
- Antheridial branch, of *Marchantia*, *277
- Antheridial cell, in pine, *318, 319
- Antheridial tube, in *Saprolegnia*, *244
- Antipodal nuclei, 142
 in embryo sac of corn, *333
- Antipodals, 334, *335, *338
- Apical notch, in fern gametophyte, *293
- Apophysis, of moss capsule, *284, *285
- Apothecia, 250, *257
- Apple, fruit of, *158
 mixed buds, 9
- Archegonia, of Bryophyta, 272
 of fern, 293, *294
 of *Funaria*, *282
 of pine, *321
 of *Riccia*, *275
 of *Selaginella*, *302, *303
- Archegonial branch of *Marchantia*, *277
- Archeporsial cells in wheat anther, *328
- Artemisia*, stem of, *67
vulgaris, leaf variation in, *345
- Ascocarp, 250
 of lichen, *257
- Ascomycetes, 229, 244, 250
 characteristics of, 249
 representatives of, 251
- Ascospore, 250
 of lichens, *257
- Ascus, 250
- Ascus fungi, 229
- Asexual reproduction, by fission, 203, 206
 by spores, 204, 206
 in Thallophyta, methods of, 206
- Ash, twigs of, *43
 winged fruit, *169
- Aspergillus*, *253, 254
- Assimilation, 1, 32, 174
- Auricles of grass leaf, *106
- Autophytic plants, 202
- Autophytic Thallophyta, 206
- Autumnal coloration of leaves, 130
- Available water in soil, 95, 186
- Avena sativa*, inflorescence and flowers of, *143
- Axile placentae, 140
- Axillary buds, *42
- Azotobacter*, 237
- B
- Bacillus, 230, *231
proteus, *231
sporogenes, *231
subtilis, *231
typhosus, *231
- Bacteria, 229, 230
 beneficial activities of, 232
 forms of, 230
 general characteristics, 230
 harmful activities of, 233
 in relation to soil fertility, 235
 multiplication of, 232
 spore formation in, 232
- Bald cypress, 188
- Barberry, leaf spines of, *129
- Bark, 46
- Barley, root of, *84, *87
 stem and leaf of, *106
- Basidiomycetes*, 229, 258
 characteristics of, 258
 representatives of, 258
- Basidiospore, 258, 265
 discharge of, *264
- Basidium, 258
 of black stem rust, *262
 of mushroom, *266
- Basidium fungi, 229
- Bast fibers, 37, 39, *53, *58, *59

Bean, 165, *166
 seed, successive stages in germination
 of, *178
Berberis vulgaris, aecidia on, *265
 leaf spines of, *129
 Berry, 156
Beta vulgaris root, storage in, 6
 Biennial, 15
 Biotic factors, 180, 181
 influence of, upon plants, 189
 Black locust, stipular spines of, *129
 Black stem rust, life cycle of, *262
 Blackberry, mixed buds, 9
 Blue mold, *253, 254
 Blue-green algae, 207
 Body cell, in pine, *318, 322
 Border parenchyma, 112, *114
 Bordered pit, *40
 Boron, 194
 Botany, definition of, 3
 Bracket fungi, *267, 268
 Bract, 133
 of pine, 313
 Branch buds, 8
 Branch roots, origin of, *90, *91, *92
Brassica rapa root, storage in, 6
Brassica, silique of, *157
 Bread mold, 245, *248, *249
 Broad bean, geotropic curvature of
 root, 12
 Bromine, 195
 Brown algae, 207, 219
 Brush, of wheat seed, 168
 Bryophyta, 197, 201
 characteristics of, 270, 271
 Buckeye, twigs of, *44
 Bud, 8
 Bud grafting, 6
 Bud scale, scar, *10, 11
 Bud scales, 5, *7
 Budding, in yeast, *255
 Buds, 6
 accessory, 7
 active, 9
 adventitious, 78

Buds, alternate, 8
 axillary, *4, 7, 8
 branch, 8
 classification of, 7, 9
 cotyledonary, *4
 dormant, 9
 flower, 8
 fruit, 8
 leaf, 8
 mixed, 8
 naked, 7
 opposite, 8
 terminal, 7
 whorled, 8
 Bulb, 5
 of onion, *76, *78
 Bundle, closed, 68, *69
 open, 68
 Bundle scar, *7, 116
 Bundle sheath, *69
 Bunt of wheat, *260
 Butternut, leaf abscission in, *116

C

Calcium, 191, 192, 194
 pectate, 18
 Calla lily, flower stalks of, *68
 Callose, 41
 Callus, 41
 Calyptra, of moss, *284
 Calyx, 135
 Cambium, 35, 47, 52, *53, 55, *58
 diagram showing differentiation of
 daughter cells, *54
 Cambium ring, 57
Capsella, 338
 development of embryo, *153
 epidermal hairs of, *112
 Capsule, *157
 Marchantia sporophyte, *280
 moss sporophyte, *283, *284, *285
 Carbohydrates, 125, 164
 manufacture of, 6
 production, rate of, 123
 Carbon cycle, 239, *240

- Carbon dioxide, 184
 apparatus demonstrating evolution of, *175
 Carolina poplar, branching of, 6
 Carotin, 21
 Carpels, *134
 Caruncle, *167
 Castor-oil plant, seedling of, *179
 seed, 166, *167
 Cedars, 309
 Cell, 2, 17-41
 from growing point of onion root, *17
 from palisade parenchyma of leaf, *17
 Cell division, 33, *34
 Cell sap, 24
 Cell wall, *17, 18, *19, *35
 Cells, multiplication of, 33
 Cellulose, 18
 Central cylinder, of roots, *90
 Characters, 344
 dominant, 350
 recessive, 350
 Chemical energy, 32
 Chemosynthesis, 237
 Cherry, buds of, 8
 flower of, *149
 Chlamydospores, *259
 Chlorenchyma, 35
 Chlorine, 195
 Chlorophyceae, 207
 characteristics of, 211
 distribution of, 211
 representatives of, 211
 Chlorophyll, absorption spectrum of, *120
 function of, 119
 Chlorophyll *a*, 20
 Chlorophyll *b*, 20
 Chloroplast, *17, *19, 20, 21, *109, *110
 Chlorosis, 194
 Chondriosomes, 19
 Chromatin, 23
 granules, *19
 Chromatophore, 20
 Chromoplast, 20, 21
 Chromosome theory of inheritance, 344
 Chromosomes, *34
 homologous, 351
 individuality, in *Crepis*, *351
 Cilia, 204, 230
 Classification, of plants, 200, 201
 of root systems, 81
 Clematis, diagram of stem, *71
 fruit of, *169
 stem of, *66
 Climatic factors, 180
 Closed bundles, 68, *69
Clostridium pasteurianum, 237
 Club mosses, 289
 Club root of cabbage, 242
 Cluster cup, of black stem rust, *262, 267
 Cockle-bur, fruit of, *169
 Coccus, 230, *231
 Coenocyte, 242
 Coenogamete, 247
 of *Rhizopus*, *250
 Coleoptile, 168, *176
 of wheat, *339
 Coleorhiza, 168, *176
 of wheat, *339
 Collenchyma, 37, *38, *53, *58
 Columella, *248, *249
 of moss capsule, *285
Comatricha nigra, *241
 Combinations, 347
 Common barberry, aecidia on, *265
 Companion cells, *40, 41, *54, *56, *69
 Complementary tissue, *64
 Compound leaf, *104, *105
 Compound pistil, 139
 Composition of soil solution, 95
 Concentration of soil solution, 95
 Conceptacles of *Fucus*, *224, *225
 Conducting tissues, 39
 Conduction of food, 76
 by roots, 97
 by stems, 70
 Conidia, *245

- Conidiophore, *245, *253
 Conidiospores, 244, *245
 development of, in *Albugo*, *246
 of blue and green molds, *253
 Conjugation, 204, 206
 in *Spirogyra*, *214, *215
 Conjugation tube, *214
 Connective, *138
 Control of stomata by the guard cells,
 109
 Cork, *37, *51, *58, *60, *64
 Cork cambium, *51, *58, *60, 64, 90
 Corm, of crocus, *77
 Corn, cross-section of stem, *69
 grain of, *163
 smut, *259
 vascular bundle, *69
 Corolla, 134
 Cortex, *53, *87
 Cortical parenchyma, *51, *53, *85,
 *92
 Cottonwood, hairy seed of, *169
 twig, two year old, *10
 Cotyledons, *4, 162, *167
 of bean seedling, *178
 of castor-oil seedling, *179
 of pine seed, 324, *325
 of wheat, *339
 Cover cells, of *Riccia* archegonium, *275
Crepis capillaris, chromosome individu-
 ality in, *351
 Crocus, corm of, *77
 Crustaceous lichen, *256
 Crystals, *23, 24
 Culms, 70
Cuscuta, 309
 a liana, 6
 Cuticle, *36, *53, 60, 106, *110
 Cuticular transpiration, 127
 Cutin, 36, 106
 Cutinized layer, 106
 Cyanophyceae, 207
 characteristics of, 207
 distribution of, 209
 representatives of, 209
 Cylindrosporium, *209
 Cytase, 173
 Cytology, 2
 Cytoplasm, *17, *19, 20
 Cytoplasmic membrane, *19, 20

 D
 Dahlia, clustered fleshy roots of, *97
 Dandelion, fruit of, *169
Darlingtonia californica, *131
 Darwin's theory of natural selection, 357
Datura, capsule of, *157
 Decay, 234
 Dehiscent fruits, 157
 de Lamarck, 356
 Delayed germination, 177
 Deliquescent type of branching, 6
Delphinium, follicle of, *157
 Denitrification, 239
 De Vries, 359
 Diastase, 173
 Diatoms, *220
 Dichotomous branching in *Fucus*, *223
 Dicotyledonae, 46
 Diffusion, 26, 27
 in relation to absorption by plant cell,
 30
 of solutes, 29
 Digestion, 172
Digitalis, stem of, *67
 Dihybrid cross, diagram to illustrate,
 *355
 Dioecious plant, 144
Diospyros, mixed buds, 9
Diplococcus, *231
 Diploid, 206
 Disc flower, *146
 Dissemination of seeds and fruits, 168
 Dodder, 309
 a liana, 6
 Dominants, 349
 Dormancy of seeds, 177
 Dormant buds, 9
 Double fertilization, 152
 Douglas fir, 310

Downy mildew, *251
Drosera, leaves of, *130
 Drupe, 157
Dryopteris, sori of, *297
 Dwarf males in *Oedogonium*, *218

E

Ecballium elaterium, fruit of, *170
 Ecology, 2
 Ectocarpus, *221, 222
 Edaphic factors, 180
 Efficiency of leaf in utilizing sun's energy, 121
 Egg cell, *136, 205
 in corn, *335
 or *Riccia* archegonium, *275
 Egg nucleus, 142
 Elaters of *Marchantia*, 278, 279
 Elder, lenticel of, *64
Eleagnus, epidermal hairs of, *112
 Elements, rôle of, in plant, 193
 Elm, winged fruit of, *169
Elodea, liberation of oxygen from, *122
 Embryo, 162, 176
 cells of pine, *324
 formation of, 152
 of corn, *338
 of pine, formation of, 322
 of *Selaginella*, *303, 304
 of wheat, *339
 sac, *139, *141, 332, *338
 sporophyte of wheat, 337
 stages in development of, in shepherd's purse, *153
 Endocarp, 156
 Endodermis, *58, *84, *85, *87, *88, *91, *92
 Endosperm, 154, 162, *167
 formation of, 153
 in corn, 338
 in wheat, 336, 338
 of castor-oil seedling, *179
 End-products of photosynthesis, 122
 Energy and materials, transformation of, 190

Energy changes brought about the plant, 195
 Energy factor, 118, 119
Enerthema papillatum, *241
 Environment, direct response to, 356
 relation of plant to, 180
 Enzymes, 172
 Epiblast of wheat, 339
 Epidermal hairs, 110, *112
 Epidermis, *36, 50, *51, 52, *53, *58, *60, *64, *69, *84, *85, *87
 of leaf, 105, 106, *107
 Epigyny, 147, *148
 Equisetineae, 289, 295
Equisetum, 295
 arvense, sporophyte of, *300
Eriobotrya japonica, fruit buds of, 8
Erysiphe graminis, *251
 Essential flower parts, 134
 European linden, leaf mosaic, *102
 Evolution, mutation theory of, 359
 and heredity, 343
 Excurrent type of branching, 6
 Exine, 150, *151
 Exocarp, 156
 External morphology of the flower, 133

F

Factors of environment, 180
 False mallow, epidermal hairs of, *112
 Fascicles, 310
 Fascicular cambium, *51, 52, *56, *58
 Fat fermentation, 234
 Fats, 164, 173
 Fermentation, 233
 acetic acid, 235
 alcoholic, 234
 carbohydrate, 234
 fat, 234
 lactic, 235
 protein, 234
 Ferns and fern allies, 288, 289
 development of sporophyte, *294
 leaf, section, of, showing sorus, *296

- Ferns and fern allies, life-cycle, diagram of, *299
 mature antheridium of, *294
 mature archegonium of, *294
- Fertilization, 152
 double, 152
 effect of, on fruit formation, 154
 in *Albugo*, *246
 in *Fucus*, 225
 in *Funaria*, 285
 in *Oedogonium*, 218
 in pine, 320, 321, 322
 in *Polypodium*, 293
 in *Riccia*, 274
 in Thallophyta, 205
 in wheat, 336
- Fibers, 38
- Fibrous root system, *81
- Ficus*, mixed buds, 9
- Fig, mixed buds, 9
- Filament, 134, *135, *136, 138
- Filicineae, 289
- Firs, 309
- Fission, 203, 206
- Flagella, 230
- Fleshy and woody Basidiomycetes, 267
- Floral leaves, 133
- Flower, 133-154
 accessory parts, 134
 bilaterally symmetrical, *144, 145
 buds, 8
 diagram of, *135, *136
 disc, of sunflower, *146
 epigynous, *148
 essential parts, 134
 external morphology of, 133
 form and arrangement of parts, 144
 hermaphroditic, 142
 histology of parts, 133
 hypogynous, *148
 incomplete, 142
 irregular, 145
 origin and development of parts, *134
 perfect, 142
 perigynous, *148, *149
- Flower, pistillate, 142
 ray, of sunflower, *146
 regular, 145
 reproductive processes of, 149
 staminate, 142
- Foliage leaf, external morphology of, 100
- Follicle, *157
- Food, 33
 conduction of, 76
 transfer of, 174
- Foot, of *Marchantia* sporophyte, *280
 of moss sporophyte, *283
- Fragaria*, aggregate fruit of, *159
 flower of, *145
 stolons of, *78, 79
- Fraxinus*, twigs of, *43
 winged fruit of, *169
- Free central placentae, 140
- Fructose, 125
 aggregate, *157, *159
 and seed, 155-179
 buds, 8
- Fruit, definition of, 155
 dehiscent, 157
 development of, 155
 fleshy, 156
 indehiscent, 157
 multiple, 159
 simple, 156
 types of, 156
- Fucoxanthin, 222
- Fucus*, *222 *223, *224, *225,
Funaria, 284
hygrometrica, female branch, *282
 male branch, *281
 life cycle of, *286
- Fungi, 229
 groups of, 229
- Funiculus, *141, 162
- G
- Galactose, 173
- Gametangia, 216
 in bread mold, 247

- Gamete, 204, 205
 of *Ulothrix*, *213
 purity of, 354
 Gametophyte, of Bryophyta, 272
 of *Marchantia*, female, *277
 of *Marchantia*, male, *277
 of moss, 284
 of pine, development of, 320
 of *Polypodium*, *292, *293
 of *Riccia*, *274
 of *Selaginella*, female, *303
 of *Selaginella*, male, *302
 of wheat, female, *331
 of wheat, male, 333, *333
 Garden cress, seedling of, *94
 Garden pea, compound leaf of, *105
 Generative cell, in pine, *318, 319
 Generative nucleus, 150, *151
 of *Lilium* microspore, *331
 Geotropism, *12, 13, 14
 Geranium, epidermal hairs of, *112
 Germ tube, 205
 Germination, conditions necessary for,
 170
 delayed, 177
 of wheat, *176
 process, 172
 Gills, *266, 269
Gloeocapsa, *208, 210
 Glumes, of wheat, *144
 Glycogen, 207
 Gnetales, 341
 Gooseberry, buds of, 8
 Grain, *163
 Grape, a liana, 6
 mixed buds, 9
 Green algae, 207, 211
 Green mold, *253, 254
 Ground cherry, fruit of, *169
 Ground meristem, 50, *51, *58
 Growing point, *4, 5, 35, *42, 83, *84, 86
 Growth, 33, 175
 Guard cells, 36, 106, *107, *108, *109,
 *110
 Gymnospermae, 45, 309
 Gymnosperms and Angiosperms, a com-
 parison, 326, 341

H

 Hairs, epidermal, 110, *112
 Halophytes, 187
 Haploid, 206
 Haustoria, 244, *245
 in *Erysiphe*, *251
 of powdery mildews, 254
 Head, of sunflower, *146
Helianthus tuberosus, flowers of, *146
 Hemi-cellulose, 125, 164, 173
 Hepaticae, 273
 Heredity, 343
 Hermaphroditic flowers, 142
 Heterocyst, 210
 Heterogamete, 205
 Heterophytic plants, 202
 Hilum, 162, *166
 Histology, 2
 Holdfast, 212, *213
 Homologous chromosomes, 351
 Hop, a liana, 6
Hordeum sativum, root of, *84, *87
 Hormogonia, 210
 Horse bean, central cylinder of, *98
 floral diagram, *144
 Horsetails, 289, 295
 sporophyte of, *300
 Host, 229
 Humidity of atmosphere, as affecting
 rate of transpiration, 126
Humulus, a liana, 6
 Hybrids, 349, 355
 Hydrophytes, 187
 Hymenium, 252
 section of, *266
 Hyphae, 242
 Hypocotyl, 163
 of bean seedling, *178
 of castor-soil seedling, *179
 of pine seed, 324, *325
 Hypogyny, 147, *148

I

- Illumination, 182
 - intensity of, 123
- Inclusions, 20, *23
- Incomplete flowers, 142
- Indehiscent fruits, 157
- Indian pipe, 309
- Indusium, of fern sporangium, *296
 - types of, 297
- Inferior ovary, *148
- Inflorescence, 135
 - of oats, *143
 - of sunflower, *146
- Inheritance, chromosome theory of, 344
- Inorganic salts, absorption of, 96
- Insectivorous plants, *130, *131, 132
- Integuments, *139, 141
 - in corn ovule, *335
 - of pine ovule, *321, *322
- Intercalary growth, 99
- Intercellular spaces, *35
- Interfascicular cambium, *51, *58, *59
- Internode, 3
- Intine, 150, *151
- Iodine, 195
- Ipomoea batatas* root, storage in, 6
- Iris, rhizomes of, *74, 78
- Iron, 191, 192, 194
- Irregular flower, 145
- Isogamete, 204

J

- Jacket cells of pine, 321
- Jerusalem artichoke, flowers of, *146
- Jimson weed, capsule of, *157
- Juglans*, buds of, 8
 - cinerea*, leaf abscission in, *116
- Junipers, 309

K

- Keel, *144
- Kelp, *222

L

- Lactic acid fermentation, 235
- Lamina, 100
- Larches, 309

- Larix*, 309
- Larkspur, follicle of, *157
- Lathyrus odoratus*, floral diagram, *144
- Leaf, 99-131
 - anatomy of, 105
 - axil, 5
 - base, 100
 - blade, 100
 - form of, 101
 - buds, 8
 - compound, *104, *105
 - diagram of cross section, *107
 - efficiency of, in utilizing sun's energy, 121
 - epidermis, *107
 - external morphology of, 100
 - fall, 116
 - form, *104
 - margin, 105
 - mosaic, *102
 - origin and development of, 99
 - physiology of, 117
 - potato, in cross section, *108
 - primary functions, 6
 - primordia, 99
 - rudiment, *4
 - scar, *7, *10, 11, 116
 - sessile, 100
 - simple, *101
 - spines of barberry, *129
 - traces, *71, *116
 - variation in *Artemisia vulgaris*, *345
 - vein system of, 115
 - venation, 100, *104
- Leaflet, *104, *105
- Leafy liverwort, *280
- Leaves, autumnal coloration of, 130
 - floral, 133
 - respiration in, 129
 - special functions performed by, 130
- Legume, flower of, *144
- Lemma, of oats, *143
 - of wheat, *144
- Lenticel, *7, *10, 11, *64
- Lepidium* seedling of, *94

Lepiota cepasestipes, *266
 Leucoplast, 20, *21
 Lianas, 6
 Lichens, *256, *257
 Life cycle, 14
 of wheat, *340
 Life history of wheat, 327
 Light, intensity, as affecting rate of
 transpiration, 127
 necessity of, for photosynthesis, 118
 Ligule of grass leaf, *106
 Lilac, powdery mildew, 252
Lilium aurantum, fertilization in, *337
 microspore of, *331
 stages in development of, *139, *140
 Lily, anther of, in section, *138
 Linin, 19, 23
 Lipase, 173
 Liquidamber, stem of, *66
 Liverworts, 273
 and mosses, 270
 leafy, *280
 representatives of, 273
 Lobed leaves, 102
Lonicera, stem of, *66
 Loose smut of oats, *261
 Loquat, fruit buds of, 8
Lupinus albus, root showing geotropic
 curvature, *13
Lycoperdon, *268
Lycopodiaceae, 289
Lycopodium, 298

M

Macrocystis, 221, 223
 Magnesium, 191, 192, 194
 Male gametophyte of pine, development
 of, 317, *318
 Male nuclei, *151
 in corn, *335, *336, *337
 Maltose, 173
Malvastrum, epidermal hairs of, *112
 Manganese, 194
 Mannose, 173

Maple, accessory buds of, 8
 samara of, *157
 winged fruit of, *169
Marchantia, antheridia of, *278
 antheridial disk of, *278
 archegonia of, *279
 archegonial receptacle of, *279
 capsule, *278, *280
 elaters, *278
 female gametophyte of, *277
 males gametophyte of, *277
 seta, *280
 sporophyte of, 278, *280
 stalk, *278, *280
 Margin of leaf, 105
 Materials and energy, transformation
 of, 190
 Materials which green plants absorb and
 changes which these materials
 undergo, 191
 Maximum temperature, 171
 Mechanical tissues, 37
 Medulla, *85, *88
 Megasporangia, of pine, *313, *316
 of *Selaginella*, 300, *301
 of wheat, 329, *330
 Megasporangiate strobili of pine, 310,
 *311
 Megaspores, of pine, *316
 of *Selaginella*, 300, *301
 of wheat, *330
 Megasporophylls, of pine, 310, *313
 of *Selaginella*, *301
 of wheat, 329
Melilotus, tap root system, 82
 Membrane, permeable, 27
 selective, 29
 semi-permeable, 27
 Mendel, Gregor Johann, 347
 Mendel's results, explanation basis of
 chromosome behavior, 350
 Mendelian inheritance, 347
Merismopedia, *208
 Meristematic tissue, 35
 Mesocarp, 156

Mesophyll, 105, 112
 Mesophytes, 187
 Micropyle, *136, *139, *141, 162, *166
 of pine ovule, *313, *321, *325
Microphaera alni, *252
 Microsporangia, of pine, 317
 of *Selaginella*, 300, *301
 Microsporangiate strobili, of pine, *315
 Microspore mother cells in wheat, *328
 Microspores, germination of, 317
 of pine, *315, 317
 stages in development of, *318
 of *Selaginella*, 300, *301, *302
 of wheat, *331
 Microsporophylls, of *Selaginella*, *301
 Middle lamella, 18, *38
 Minimum temperature, 171
 Mitosis, 33, 34
 Mixed buds, 8
 Modifications, 346
 of stem, 78
 Monocotyledon type of stem, 67
 Monocotyledonae, 46
 Monoecious plant, 144
 Monohybrid cross, diagram to illustrate,
 *349
Monotropa, 309
 Monterey pine, 311
 Morphology, 2
Morus, mixed buds, 9
 Mosaic, *102
 Moss, life-cycle diagram of, *286
 Moses, 281
 Movement of water in soil, 95
 Mulberry, mixed buds, 9
 Multiple fruit, 159
 Multiplication of cells, 33
 Musci, 281
 Mushroom, *268
 Mustard seedling, showing phototropic
 curvature, *13
 Mustard, silique of, *157
 Mutants, 359
 Mutation theory of evolution, 359
 Mutations, 346

Mycelium, 244
 Myxomycetes, 229, *241
 characteristics of, *241

N

Natural selection, theory of, 357
 Neck, of archegonium, 274, *275
 Neck canal of *Riccia* archegonium, *275
 Nectar gland, *136
Nepenthes villosa, *131
 Net venation, 100, *103
 Nitrification, 238
 Nitrobacter, 238
 Nitrogen, 191, 192, 193
 Nitrogen cycle, *236, 239
 Nitrogen fixation, 235, 236
Nitrosomonas, 238
 Node, 3
Nostoc, *209, 210, 215
 Nucellus, *139, *141
 in corn ovule, *335
 of pine, *316
 of wheat ovule, *330
 Nuclear membrane, *17, *19, 22
 Nuclear net, *17, 22
 Nuclear sap, 22
 Nucleus, *17, *19, 20, 22
 of pine ovule, *321, *325
 Nucleolus, *17

O

Oak, acorn of, *159
 mixed buds, 9
 Oat smut, *261
 Oats, inflorescence and flowers of, *143
Oedogonium, 3, *216, *217, *218
 germination of oospore, *219
 Oil vacuoles, 24
 Oils, 125
 Onion, bulb of, *76, 78
 Oogonium in *Oedogonium*, *218
 Oomycetes, 242
 Oospore, 205
 Open bundles, 68
 Operculum, of moss capsule, *284, *285

Opposite buds, 8
 Optimum temperature, 171
 Organ, 1
 Organic evolution, theory of, 198, 199
 Organs and tissues, 1
 Origin of species, theories as to, 356
 Orthogenesis, 357
Oscillatoria, *210, 215
 Osmotic pressure, 28
 Ovary, 134, *135, *136, *137, *139
 inferior, *148
 superior, *148
 Ovules, 140
 coats, *136
 longitudinal section of lily, *141
 of pine, *313, *321
 stages in development of, *139, *140
 Oxygen, 191, 193
 rôle of, in germination, 171

P

Palet, of oats, *143
 Palisade parenchyma, *107, *108, *110, 112
 Palmately lobed leaf, 103, *104
 Palmately veined leaf, 101
Papaver, capsule of, *157
 Parallel venation, 100, *103
 Paraphyses, 252
 Fucus, *224, *225
 Funaria, *281
 lichen, *257
 Parasite, 229
 Parenchyma, *35
 Parietal placentae, 140
Parmelia perlata, *257
 Parthenocarp, 156
 Pea, pod of, *157
 Peach, buds of, 8
 Pear, mixed buds, 9
 simple leaf, *101
 Pectin, 18
 Pectose, 18
 Pedicel, *135
 Peduncle, 135

Pelagophycus, *222
Pelargonium, epidermal hairs of, *112
Penicillium, *253, 254
 Perennial, 16
 Perfect flowers, 142
 Perianth, 135
 of *Marchantia* sporophyte, *280
 Pericarp, 156
 Pericycle, *51, 52, *53, *58, *84, *85, *87, *88, *91, *92
 Periderm, *116
 Perigyny, 147, *148, *149
 Peristome, of moss capsule, *285
 Perithecium, 251
Peronospora, *251
 Persimmon, mixed buds, 9
 Petal, *134, *135, 138
 Petiole, anatomy of, 115
Peziza, 250, 251
 aurantiaca, 252
 Phaeophyceae, 207
 characteristics of, 219
 distribution of, 222
 representatives, 222
Phaseolus, climbing stem, 6
 successive stages in germination of seed, *178
 vulgaris, seed of, *166
 Phellogen, 57, *64, 90
 Phloem, 52, 54, *56, *58, *85, *87, *88
 parenchyma, *53
 Phosphorus, 191, 192, 193
 Photosynthesis, 6, 32, 117
 and respiration, 31, 32
 by-products of, 121
 conditions influencing rate of, 123
 course of, 123
 end-products of, 123
 energy factor in, 119
 necessity of light for, 118
 utilization of the product of, 124
 Phototropic curvature, *13
 Phototropism, 14
 Phycocyanin, 208
 Phycoerythrin, 226

- Phycomycetes, 229, 242
 characteristics of, 242
 representatives of, 242
Phylloxera, 190
Physalis, fruit of, *169
 Physiology, 2
Picea, 309
Pileus, *266, 269
Pimpernel, sessile leaf of, *101
Pine, winged seed of, *169
Pines, 309
 life history of, 310
Pinnately lobed leaf, 103, *104
Pinnately veined leaf, 101
Pinus, 309, 310
 and *Selaginella*, a comparison, 324
 cones of, 310, *311, *312, *313, *314
 fertilization in, 320
 lambertiana, cone of, *312
 megasporophylls of, *313
 microsporophylls of, *313, *314, *315
 pollination in, 319
 radiata, 311
 sporangia of, 316, 317
 sporophyte of, 310
 strobili of, 310, *311, *312, *313, *314
 strobis, resin duct of, *73
 winged seed of, *169
Pistil, 134, *135, 139
 compound, 139
 simple, 139
Pistillate flowers, 142
Pisum sativum, compound leaf of, *105
 pod of, 157
 tendrils of, 11
Pith, 47, *51, 52, *53, 54, *58
Pith cells, *56
Pith ray, *51, 52, 54, *58, *59
Pith ray cells, *56
Pitted tracheal tube, *53, *69
Placenta, 140
Placentation, 140
Plant bodies, kinds of, 3
Plant body, 1
 of seed plants, 3
Plant roods, conduction of, 5
Plant kingdom, classification of, 201
Plant relationships, meaning of, 197
Plants, classification of, 200
Plasmodia, 241
Plasmodiophora, 242
Plasmolysis, *31
Plastid, *17, 20
Platanus, stem of, *66
Plumule, 162, *167
 of bean seedling, *178
 of castor-oil seedling, *179
 of pine seed, 324, *325
 of wheat, *339
Pod, of pea, *157
Polar nuclei, *136, 142, 334, *335, *336, *337
 in embryo sac of corn, *333
Pollen grain of wheat, *331
Pollen grains, *150
 germination of, *151
Pollen sac, *136, *138
Pollen sacs, of pine, *315
Pollen tube, *136
 formation of, 151
 in corn, *335, *336
 of pine, *321
Pollination, 149, 150
 and development of pollen tube in
 wheat, 334
 in pine, 319
 insect, 150
Polygamous species, 144
Polypodium, 292
 development of gametophyte of, *292
 life-cycle diagram of, *299
 sori of, *297
Polyporus squamosus, *267
Polysiphonia, *227
Polystichum, sori of, *297
Pome, 157, *158
Poppy, capsule of, *157
Populus, hairy seed of, *169
Porcupine grass, fruit of, *169
Porella, *280

Potassium, 191, 192, 194
 Potato, flower of, *147
 fruit of, *147
 leaf of, in cross section, *108
 tuber and sprouts, *75
 Powdery mildews, *251, 254
 ascus in, *252
 Precipitation and atmospheric humidity,
 184
 Primary cortex, *51, 52, *58, *60
 Primary endosperm nucleus, 152
 Primary growth of dicotyledon stem,
 *58
 Primary meristems, 50, *58
 Primary permanent tissues, 50
 Primary phloem, *51
 Primary root system, 81
 Primary roots, 80
 Primary xylem, *51
 Primordial meristem, *51, *58
 Procambium cylinder, *51, 52
 Procambium strands, 50, *51, *58, *84
 Pro-embryo of pine, 322, *323, *324
 Promycelium, *259
 of black stem rust, *262
 Propagation by means of stems, 77
 Proteases, 173
 Protein fermentation, 234
 Proteins, 125, 164, 165, 173
 Prothallial cell, in *Selaginella*, *302
 Prothallium, of fern, *293
Protococcus, 3, 211, *212
 Protoderm, 50, *51, *58, 86
 Protonema, 285
 Protophloem, *69
 Protoplasm, 17
 Protoplast, 17, 18, 19
Prunus, buds of, 8
 cerasus, flower of, *149
Psalliotia campestris, *264
Pseudomonas radicola, 237
 Pseudopodia, 241
Pseudotsuga, 310
 Pteridophyta, 197, 201, 288
 advance of over Bryophyta, 306

Pteridophyta, classes of, 289
Pteris, sori of, *297
Pterosiphonia, *227
Puccinia, 261
 graminis, *262
 Puff-balls, *268
 Putefraction, 234
 Pyrenoid, *214, *218

Q

Quercus, mixed buds, 9
 rubra, sections of wood, *63
 suber, 37

R

Rachilla, of oats, *143
 Rachis, 105
 of wheat, spikelet, *144
 Radial symmetry, 145
 Radicle, 80, 163, *167
 of pine seed, 324, *325
Rafflesia arnoldii, 11
 Raphe, 162, *166
 Raphides, 24
 Raspberry, aggregate fruit of, *157
 Raw materials, 117
 conduction of, 5
 for food manufacture, 33
 Ray flower, *146
 Receptacle, *135
 of *Marchantia*, *279
 Recessives, 347
 Red algae, 207, 226
 Red oak, sections of wood, *63
 Reduction division, 206
 Redwood, 310
 cross section of log, *47, *48
 Region of elongation, of root, 83, *84,
 85, 86
 of root hairs, 83, *84, 85, 86
 Regular flower, 145
 Relation of plant to environment, 180
 Reproduction, asexual, by fission, 203
 by spores, 204, 206
 by means of roots, 98
 sexual, 204, 206

- Reproductive activities, 1
 Reproductive processes of flowers, 149
 Resin duct, of pine, *73
 Respiration, 1, 174
 and photosynthesis, 31, 32
 in leaves, 129
 Rhizoids, of Bryophyta, 270
 of fern gametophyte, *293
 of *Marchantia*, *277, *278, *279
 of *Selaginella*, *302
 Rhizomes, 5
 of iris, *74, 78
 of potato, *75
 Rhizophore, of *Selaginella*, *301
Rhizopus nigricans, 245, *248, *249
 Rhodophyceae, 207
 characteristics of, 226
 distribution of, 227
Ribes, buds of, 8
Riccia, 278
 antheridium of, *274
 archegonium of, *275
 diagram of life cycle, *276
 thallus of, *273
Richardia, flower stalks of, *68
Ricinus communis, seed of, *167
 seedling of, *179
 Rise of sap, 73
Robinia pseudacacia, development of
 tracheal tube, *55
 stipular spines of, *129
 Rôle of chemical elements, 193
 Root, 3, 80-97
 anatomy of, 86-88
 branching, 90
 cap, *4, 5, 83, *84, *92
 external features of, 83
 origin of branch, diagram, *90, *91,
 *92
 primary functions of, 5
 secondary increase in thickness, dia-
 grams, *89
 tip, 86
 Root hairs, *84, 91, 92, *94
 stages in development, *93
 Root systems, classifications of, 81
 form of, 82
 Roots, anchorage by, 97
 and stems, difference between, 80
 clustered fleshy, *97
 conduction by, 97
 functions of, *92
 growth in diameter of, 88
 kinds of, 89
 reproduction by means of, 98
 storage by, 97
 structure of, 83
Rubus, aggregate fruit of, *157
 mixed buds, 9
 Runner, 5, *78, 79
 Rusts, 260
- S
- Saccharomyces cerevisiae*, *255
 Samara, *157
Sambucus, lenticel of, *64
 Sap, rise of, 73
Saprolegnia, *243, *244
 Saprophyte, 229
Sarcina, *231
Sarracenia variolaris, *131
 laciniata, *131
 Scarlet runner bean, climbing stem, 6
 Schizomycetes, 229
Sclerotinia, 250
 Scouring rush, 295
 Scutellum, 168, 337
 Sea lettuce, 3
 Secondary cortex, *51, *58, *60
 Secondary growth, in woody dicoty-
 ledon-gymnosperm stem, 57
 of dicotyledon stem, *58
 Secondary meristems, 64
 Secondary phloem, *51
 Secondary roots, 80
 Secondary xylem, *51
 Sections of stems, kinds of, *46
 Seed, 160
 coats, 162, *167
 descriptions of representative types,
 165

- Seed, development of, 153, 160, 161
 dissemination of, 168
 kinds of food stored in, 164
 leaves, 162
 of wheat, *341
 structure of, 161
- Seed plant, diagram showing principal organs, *4
- Seedling, of garden cress, *94, 178
- Seeds, conditions affecting vitality of, 177
 dormancy of, 177
 of pine, *313, 323
- Segregation, 354
- Selaginella*, 296, 298
 and *Pinus*, a comparison, 324
- Selective membrane, 29
- Semi-permeable membrane, 20, 27, 28
- Senecio mikanoides*, leaf of epidermis, *107
- Sepals, *134, 135, 137
- Sequoia*, 310
sempervirens, cross section of log, *47, *48
- Sessile leaf, 100, *101
- Seta, of *Marchantia* sporophyte, *280
 of moss sporophyte, *283, *284, *285
- Sexual reproduction in Thallophyta, 204
- Shade plants, 183
- Sheath of grass leaf, *106
- Shepherd's purse, development of embryo, *153
 epidermal hairs of, *112
- Shoot, 3
 climbing, 6
 deliquescent, 6
 erect, 6
 excurrent, 6
 general external features of, 6
 prostrate, 6
- Sieve plate, *40, 41, *53, *69
- Sieve tubes, 39, *40, *53, *54, *56
- Silicon, 195
- Silique, *157
- Simple fruits, 156
- Simple pistil, 139
- Sinuses, of leaf, 102, 103
- Slime fungi, 229
- Smuts, 259
- Sodium, 195
- Soil, air in, 187
 conditions, as affecting rate of transpiration, 127
 fertility, bacteria in relation to, 235
 solutes, quantity and nature of, 188
 solution, concentration of, 95
 composition of, 95
 temperature, 188
- Solanum tuberosum*, flower of, *147
 fruit of, *147
 leaf of, in cross section, *108
- Solar energy, 32
- Solutes, diffusion of, 29
- Solution, 25
- Solvents, passage of, through membranes, 26
- Sorus, 261
 of fern, *296
 of ferns, types of, *297
- Special creation, theory of, 198
- Spectrum, 119
 absorption, *120
 evidence of relative effectiveness of different parts of, 120
- Sperm, 205
- Sperm nuclei, *151
 of pine, 322
- Spermagonia in black stem rust, 266
- Spermatia in black stem rust, 266
- Spermatophyta, 197, 201, 307
 chief distinguishing characteristics of, 308
 classes of, 45, 309
- Spikelet, of oats, *143
 of wheat, *144
- Spines, leaf of barberry, *129
 stipular of black locust, *129
- Spireme, 34
- Spirillum*, 230, *231
undulum, *231

- Spirochaete, *231
Spirogyra, 3, *214
 Spongy parenchyma, *107, *108, 112, *114
 Sporangia of bread mold, *248, *249
 Sporangiophore of bread mold, *248, *249
 Spores, asexual reproduction by, 204
 Sporidium, *259, *262
 Sporogenous cells in wheat anther, *325
 Sporophylls of fern, 298
 Sporophyte, of Bryophyta, 272
 of common horsetail, *300
 of fern, 294, *295
 of moss, *283, *284
 of pine, 310
 of *Riccia*, *275
 of wheat, 341
 Spruces, 309
 Squinting cucumber, fruit of, *170
 Stalk cell, in pine, *318, 322
 Stamens, 134, *135, *136, 138
 Staminate flowers, 142
 Standard, *144
Staphylococcus, *231
 Starch, 125, 164, 173
 digestion, *173
 Starch grains, 21, 24
 kinds of, *165
 Stems, 42-79
 aerial, 12
 and roots, differences between, 80
 and leaves, functions of, 5
 modified, 11
 principal distinctions between, 3
 at growing point, 50
 coniferous, diagram of, *62
 functions of, 70
 growth and development of, *44
 hardwood, diagram of, *61
 herbaceous dicotyledon, 45
 type, 65
 modifications, 78
 monocotyledon, 45
 type, 67
 Stemonitis fusca, *241
 Sterigma, 258, *259, 265
 St. Hilaire, Geoffrey, 356
 Stigma, 134, *135, *136, *137, 139
 Stigmatic fluid, 151
 Stinking smut of wheat, *260
 Stipa, fruit of, *169
 Stipe, *266, 269
 Stipular spines of black locust, *129
 Stipules, 100, *101
 Stolon, *78, 79
 in bread mold, 246, *248
 Stomata, 36, *107, *108, *109
 control of, by guard cells, 109
 of moss capsule, *285
 Stomatal transpiration, 127
 Stone cells, 37, 39
 Storage, by roots, 97
 in stems, 77
 Strawberry, aggregate fruit of, *159
 flower of, *145
 stolons of, *78, 79
 Streptococcus, *231
 Strobili, carpellate, 310, *311
 megasporangiate, 310, *311
 microsporangiate, 310, *315
 of fern, 298
 of pine, 310, *311
 of *Selaginella*, *301
 staminate, 310, *315
 Style, 134, *135, *136, *137, 139
 Suberin, 37
 Sub-stomatal air chamber, *110
 Subterranean stems, 12
 "Suckers," 98
 Sucrose, 125
 Sugar pine, cone of, *312
 Sugar-beet root, storage in, 6

Sugars, 164
 Sulphur, 191, 192, 194
 Sun plants, 183
 Sundew, leaves of, *130
 Sun's energy, efficiency of leaf in utilizing, 121
 Superior ovary, *148
 Support, function of stem, 70
 Suspensor cells, of pine, 322, *323, *325
 of *Rhizopus*, *250
 of *Selaginella*, *303, *304, 305
 Sweet clover, tap root system, *82
 Sweet pea, floral diagram, *144
 tendrils of, 11
 Sweet potato, modified root, 11
 root, storage in, 6
 Symbiosis, 238
Synechococcus, *208, 209
 Synergid nuclei in embryo sac of corn, *333
 Synergids, 142, 334, *335, *336
 and antipodal nuclei, fate of, 152
 Systematic botany, 3

T

Tap root system, 81, *82
 Tapetum in wheat anther, *328
 Taraxacum, fruit of, *169
Taxodium distichum, 188
 Taxonomic botany, 3
 Tegmen, 162
 Teleutospores, *262, *264, 265
 Temperature, 181
 as influencing rate of photosynthesis, 123
 of soil water, 95
 rôle of, in germination, 171
 Tendrils, 79
 Terminal bud, *4, *42
 opening of, *43
 Testa, 162
 Tetrads, in Bryophyta, 272
 Thallophyta, 197, 201, 203

Thallophyta, characteristics of, 203
 methods of reproduction in, 206
 Thallus, of *Marchantia*, *277
 of *Riccia*, *273, *274
 Theories as to the origin of species, 356
 Theory, of natural selection, 357
 of organic evolution, 198, 199
 of special creation, 198
Thiospirillum, *231
Tilletia, *260
 Tissue, 2
 Tissues, 33, 35
 meristematic, 35
 origin and development of, 50
 Tracheal tubes, 39, *56
 development of, *55
 Tracheids, 39, *40, *56, *57
 of leaf, *114
 Transformation of energy and materials, 190
 Transpiration, 1, 6, 93
 and transpiration stream, 125
 conditions affecting rate of, 126
 cuticular, 127
 demonstrating lifting power of, *72
 external factors which affect rate of, 126
 internal factors which affect rate of, 127
 means of reducing, 127
 pull, 75
 rate of, 96
 stomatal, 127
Triticum, a life history of, 327
 spikelet of, *144
 Tropisms, 14
 True solution, 25
 Tube nuclei, 150, *151
 in corn, *335
 in *Lilium* microspore, *331
 in pine pollen, *318
 Tuber, 5, *75, 78
 of potato, 11
 Turgor pressure, 30
 Turnip root, storage in, 6

U

- Ulmus, winged fruit of, *169
- Ulothrix*, 212, *213
- Ulva*, 3
- Union of flower parts, 146
- Uredosorus, *262, 263
- Use and disuse, 356
- Ustilago avenae*, *261
 - levis*, *261
 - maydis*, 259
- Utricularia vulgaris*, roots wanting, 11

V

- Vacuole, *17, *19, 20, 24, 31
- Variation, 343
 - kinds of, 346
 - leaf, *345
- Vascular bundles, 52, *58, *59, *69
 - cross section, *56
 - of corn, *69
 - of leaf, 115
- Vascular cambium, 57
- Vascular rays, 60
- Vascular tissue, 54
- Vegetative activities, 1
- Vegetative and reproductive functions, 133
- Vegetative nucleus, in pine, 318, *319
- Vein system of leaf, 115
- Venation, 100
 - types of, 100, *103
- Venter, of archegonium, 274, *275
- Ventral canal cell of *Riccia* archegonium, *275
- Vibrio cholerae*, *231
- Vicia faba*, central cylinder of, *88
 - floral diagram, *144
 - geotropic curvature of root, 12
- Violet, capsule of, *157
- Vitality of seeds, conditions affecting, 177
- Vitis*, a liana, 6
 - mixed buds, 9

W

- Walnut, buds of, 8
- Water, 191, 192
 - absorption of, 93
 - absorption and germination, 172
 - as agency in disseminating seeds, 168
 - available in the soil, 95, 186
 - bladderwort, roots wanting, 11
 - cohesion, *75
 - factors affecting intake from soil, 95
 - mold, 243
 - movement in soil, 95
 - rôle of, in germination, 171
- Wheat, anther of, *328, *329
 - embryo of, *339
 - embryo sac of, 332
 - endosperm in, 338
 - female gametophyte of, 332, *333
 - fertilization in, *336
 - fibrous root system, *81
 - grain of, *163
 - life-cycle diagram, 340
 - life history of, 327
 - male gametophyte of, *331
 - megasporangia of, 329
 - megaspores of, *329
 - megasporophylls of, 329
 - microsporangia of, 328
 - microsporophylls of, *328
 - pollination in, 334
 - seed of, 168, 341
 - spikelet of, *144
 - stages in germination of, *176
- White lupine, root showing geotropic curvature, *13
- White rust of crucifers, 244, *245, *246
 - *247
- Whorled buds, 8
- Wind, 168, 185
- Wing, *144
- Wolffia*, 11
- Wood, 46, 56
 - fibers, 37, 39, *53
 - parenchyma, *53
 - rays, 50

Woodwardia, sori of, *297

Woody dicotyledon—gymnosperm type
of stem, gross features of struc-
ture, 46

X

Xanthium, fruit of, *169

Xanthophyll, 21

Xerophytes, 187

Xylem, 52, *56, *58, *85, *87, *88

Y

Yeast, 254, *255

reproduction in, *255

Z

Zea mays, cross section of stem, *69

Zea mays, grain of, 163

vascular bundle, 69

Zinc, 194

Zoosporangia in *Ectocarpus*, *221

in *Saprolegnia*, *243

Zoospores, 204, 206

Saprolegnia, *243

Ulothrix, *213

Zygomycetes, 242

Zygospore, 204

in *Spirogyra*, *214, *215

of *Rhizopus*, *250

of *Ulothrix*, *213

Zygote, 152, 203

in corn, *338

Zymase, 173, 256

Shall ophytes Characteristic of each division
algae " " " " Class
Classes
Fungi The Life Cycle of a Typical
Classes. " " " " each division

3 Bryophytes
3 Pteridophytes

A. Dry Fruits (Pericarp dry)

1. Dehiscent fruits (splitting open when ripe)
 a. Legume or true pod. - carpel one
 b. Follicle - carpel one -
 c. Capsule - carpels two or more -
 1. along line of union (septa)
 2. " Middle of carpel (Locuticid)
 3. " " " " " "

$$\begin{array}{r} 17 \\ 30 \\ \hline 64 \end{array}$$

▷ Silique - carpels two -

2. Ende hiscent

- a. Akene.
b. grain
c. Samara (Key fruit.)
d. Shizocarp.
e. Nuts.

1. Hickory nut, Walnut, Butternut,
2. Hazel nut, Chesnut,
3. Acorn cup,

B. *Fleshy fruits (Pericarp fleshy)*
1. *Orange*

1. Drupe
2. Pome.
3. Berry.
4. Aggregate fruits
5. Multiple "

